

CRETACEOUS FAUNAS FROM ZULULAND AND  
NATAL, SOUTH AFRICA. THE AMMONITE FAMILIES  
NOSTOCERATIDAE HYATT, 1894 AND  
DIPLOMOCERATIDAE SPATH, 1926

by

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(With 64 figs)

[MS submitted August 2001]

[MS accepted 31 January 2002]

## ABSTRACT

Some of the Upper Cretaceous heteromorph ammonites from Zululand and Pondoland, which had previously been described by Klinger (1976), are revised and refigured. New material and taxonomic data are incorporated in the present descriptions. The provisional classification adopted here is loosely based on that of Wright (1997) pending a full review of the relationships between the families Diplomoceratidae and Nostoceratidae. Representatives of the genera and subgenera *Eubostrychoceras* (*Eubostrychoceras*) Matsumoto, 1967, *E. (Amapondella)* Klinger & Kennedy, 1997, *Nostoceras* (*Nostoceras*) Hyatt, 1894, *Nostoceras (Bostrychoceras)* Hyatt, 1900, *Didymoceras* (*Didymoceras*) Hyatt, 1894, *Didymoceras (Eodidymoceras)* s. gen. nov., *Diplomoceras* Hyatt, 1900, *Glyptoxoceras* Spath, 1925, *Scalarites* Wright & Matsumoto, 1954, *Neoglyptoxoceras* Collignon, 1969, *Neocrioceras* (*Neocrioceras*) Spath, 1921b, *N. (Schlueterella)* Wiedmann, 1962, *Pseudoxybeloceras* (*Pseudoxybeloceras*) Wright & Matsumoto, 1954 and *Spiroxybeloceras* Kennedy & Cobban, 1999, are described, including the following new species: *Eubostrychoceras (Eubostrychoceras) nibelae* sp. nov., *E. (E.) zulu* sp. nov., *Didymoceras (Didymoceras) australis* sp. nov., *Didymoceras (Didymoceras?) africanum* sp. nov., *Didymoceras (Eodidymoceras) howarthi* sp. nov., *Neoglyptoxoceras collignoni* nom. nov., and *Neocrioceras (Neocrioceras) annelisae* sp. nov.

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## INTRODUCTION

In 1976 Klinger described most of the known heteromorph ammonites from Zululand and Pondoland\*, excluding the scaphitids and most of the baculitids. Unfortunately, during the editing process, reduced format working copies of the plates were substituted for the original plates. Consequently, the actual published figures were much smaller than the originals and of unsatisfactory quality. In this present contribution we refigure some of the 1976 material belonging to the families *Nostoceratidae* and *Diplomoceratidae*, as well as new material collected in the interim. Also, taxonomic changes and/or corrections are incorporated.

## LOCATION OF SPECIMENS

The following abbreviations are used to indicate the location of specimens mentioned in the text.

GD Centre des Sciences de la Terre, Université de Bourgogne, Dijon  
NMB National Museum, Bloemfontein  
SAM South African Museum  
SAS Council for Geosciences, Pretoria

## FIELD LOCALITIES

Details of field localities are given by Kennedy & Klinger (1975); further descriptions of these localities are deposited in the Geological Collections, Oxford University Museum of Natural History, Department of Palaeontology, Natural History Museum, London and Division of Earth Sciences, South African Museum, Cape Town.

## SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916), reviewed by Kullmann & Wiedmann (1970) is followed here: I = internal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

## DIMENSIONS

Dimensions are given in millimetres. Wb = Whorl breadth; Wh = Whorl height; Wb:Wh = ratio of whorl breadth to whorl height. Prefixes M<sub>x</sub> and M<sub>n</sub> indicate maximum and minimum measurements. Ri = Rib index, ribs counted along the length of the specimen over a distance equal to the whorl height measured at the middle of that distance.

\*In current geopolitical terminology, Zululand and Pondoland now form parts of the provinces of KwaZulu-Natal and Eastern Cape respectively. For the sake of continuity, we retain the names Zululand and Natal in the titles of our series of systematic descriptions of the ammonites from these regions.

## CLASSIFICATION

Various attempts have been made to classify the genera referred to the families Nostoceratidae and Diplomoceratidae (amongst others Spath 1953; Wright 1957, 1997; Anderson 1958; Matsumoto 1959, 1967, 1977; Wiedmann 1962; Howarth 1965; Klinger 1976, 1982; Ward 1976; Ward & Mallory 1977; Cooper 1994). Broadly speaking, the genera were either lumped together or the families were split into numerous genera and subgenera, based on minute differences. None of these classifications corresponded and were neither satisfactory nor consistent. Reasons for this can be ascribed to many factors. Because of the loose coiling in most of the taxa, complete specimens are rare. The shells may be broken due to predation, taphonomic processes and during preparation from the matrix. Consequently, some genera were based on fragments and their diagnoses were incomprehensible. Furthermore, there is an extreme range of variation, not only within the same species, but in genera. In some, ornamentation was accorded priority, whereas in others the coiling was regarded as diagnostic. We are still not certain of the significance of the different coiling strategies of the early ontogenetic stages. To add to this, the Nostoceratidae and Diplomoceratidae show a rapid rate of evolution. Finally, dimorphism also has to be taken into consideration.

On completion of this largely descriptive section, we intend to publish a separate part on the classification and origins of the families Nostoceratidae and Diplomoceratidae, based on study of actual material at our disposal from various parts of the world. This is to be accompanied by an annotated list of species referred to the families, similar to that provided by the authors' description of the family Baculitidae Gill, 1871 (Klinger & Kennedy 2001).

For the purpose of description of the South African material below, we provisionally use a classification adapted from Wright (1997) with a few modifications.

## SYSTEMATIC PALAEONTOLOGY

Suborder ANCYLOCERATINA Wiedmann, 1966

Superfamily TURRILITACEAE Gill, 1871

Family **Nostoceratidae** Hyatt, 1894

(= Jouaniceratidae Wright, 1952; Bostrychoceratinæ Spath, 1953;

Hyphantoceratinæ Spath, 1953; Emperoceratinæ Spath, 1953;

Proavitoceratinæ Spath, 1953 *errore pro* Pravitoceratinæ)

Genus *Eubostrychoceras* Matsumoto, 1967

### *Type species*

*Eubostrychoceras indopacificum* Matsumoto (1967: 333, pl. 18 (fig. 1)) by original designation of Matsumoto (1967: 332).

### *Diagnosis*

Early ontogeny may be irregular, consisting of straight shaft(s) or heterostrophic

whorls, followed by helically coiled stage that is either loosely or tightly coiled or a combination of both, and of variable duration, ending in a body chamber which may face upwards or embrace part or all of the helix. Ornament consists of simple ribs, in some with intercalated flared ribs at some stage or other. Tubercles generally absent.

### Discussion

Two subgenera are here referred to *Eubostrychoceras*, *E. (Eubostrychoceras)* and *E. (Amapondella)* Klinger & Kennedy 1997. *Eubostrychoceras* (*Eubostrychoceras*) may have heterostrophic or hamitid to ptychoceratitid early whorls, followed by loosely or tightly coiled helical whorls. Ornament in most species consists of simple ribbing only; *E. (E.) japonicum* differs in having flared ribs in early and late ontogeny and incipient tuberculation. *Eubostrychoceras* (*E.*) *auriculatum* (Collignon, 1965) (Figs 3C, 7B–C) has flared ribs on the body chamber.

*Eubostrychoceras* (*Amapondella*) Klinger & Kennedy, 1997, differs from the nominal subgenus in having intercalated flared ribbing on part of the phragmocone and on the body chamber; the latter coils upwards and over the apex of the helical stage.

### Subgenus *Eubostrychoceras* (*Eubostrychoceras*) Matsumoto, 1967

#### Type species

*Eubostrychoceras* (*Eubostrychoceras*) *indopacificum* Matsumoto (1967: 333, pl. 18 (fig. 1)), by original designation of Matsumoto (1967: 332).

#### Diagnosis

Early ontogeny consists of one or two, possibly three straight shafts; in rare cases heterostrophic, followed by helical whorls, either in close contact or loose, corkscrew-like. Aperture simple, facing obliquely upwards. Ornament in most species consists of simple ribbing and periodic constrictions. Suture moderately complex. Siphuncle situated at mid-flank.

#### Discussion

When Matsumoto (1967: 332) initially erected this (sub)genus, he included only forms with contiguous whorls, and with an upward-facing aperture that does not detach itself from the base of the spire. He also mentioned that the early whorls may show slightly irregular coiling and change in direction of ribbing. The type species, *E. (Eubostrychoceras) indopacificum* from the Coniacian of Japan, Madagascar and India (see e.g. Boule *et al.* 1907, pl. 7 (14) (fig. 1)) or Kennedy (1986, text-fig. 36)), shows the characters of the genus. Later, however, Matsumoto (1977: 324–329) expanded the scope of *Eubostrychoceras* s.s. to also include species with loosely coiled, helical whorls, as well as those with a detached, recurved body chamber. Essentially, *Eubostrychoceras* s.s. as interpreted subsequently by Matsumoto (1977) included virtually all the non-tuberculate species that had originally been referred to the genus *Bostrychoceras* Hyatt, 1900 except for the type species, *Bostrychoceras polyplocum* (Roemer, 1841).

Taxonomy within *Eubostrychoceras* s.s. is not easy. Wiedmann (1962: 202) included virtually the whole of what we regard here as *E. (Eubostrychoceras)* in a single 'super-species', *Cirroceras (C.) indicum*. This he divided into three subspecies based mainly on density of ribbing: *C. (C.) indicum saxonicum* (Schlüter, 1875) with 90 ribs per whorl, *C. (C.) indicum indicum* (Stoliczka, 1866) with 50 ribs per whorl and *C. (C.) indicum elongatum* (Whiteaves, 1903) with 25 ribs per whorl. This approach was initially adopted in describing the KwaZulu material by Klinger (1976), but in retrospect, we realize that Wiedmann's approach was unrealistic from both a taxonomic and stratigraphic point of view. Loosely and tightly coiled forms were included in the same subspecies and, even by heteromorph standards they had extremely long stratigraphic ranges—Turonian to Campanian.

We follow a more conservative interpretation of the subgenus. Based on coiling and ornamentation, two more or less distinct species groups can be recognized in the expanded subgenus *E. (Eubostrychoceras)*.

1. Group of *E. (Eubostrychoceras) indopacificum*. This includes nearly all the species originally included in *Eubostrychoceras* by Matsumoto (1967). Except for the very early whorls, discussed above, the greater part of the shell consists of a tightly coiled spire, ornamented by non-tuberculate ribs and constrictions only, ending in a slightly upwards facing aperture.
2. Group of *E. (Eubostrychoceras) otsukai* (Yabe, 1904) as interpreted by Collignon (1969). This group is easily identified by the generally loose, corkscrew-like coiling in the main part of the shell. The early whorls could be straight and in line with the axis of coiling, but not enclosed in the helix. The aperture also faces obliquely upwards.

#### Occurrence

*Eubostrychoceras (Eubostrychoceras)* first occurs in the lower Turonian, but only becomes common in the upper Turonian and persists through the Coniacian to the Campanian. The youngest possible *E. (Eubostrychoceras)* is a fragment recorded from the Maastrichtian of Nigeria by Reyment (1955: 15, pl. 1 (fig. 4)) as *Bostrychoceras* sp.

The genus is best known from the middle Turonian to the Campanian, with records from Japan, India, Madagascar, KwaZulu, North Africa, West Africa, Western Europe, the Pacific Coast of North America, and from the U.S. Western Interior.

#### *Eubostrychoceras (Eubostrychoceras) indopacificum* Matsumoto, 1967

Fig. 1D–G

1895 *Turrilites (Heteroceras) indicus* Kossmat (non Stoliczka), p. 143 [47], pl. 20 [6] (figs 5a–c, 6).

1907 *Turrilites (Bostrychoceras) polyplocus* Boule *et al.* (non Roemer), p. 61 [41], pl. 14 [7] (figs 1–2).

1926 *Bostrychoceras indicum* Stoliczka; Tokunaga & Shimizu, p. 193, pl. 22 (fig. 4a–b), pl. 26 (figs 1–10).

1965 *Bostrychoceras indicum* Stol.; Collignon, p.10, pl. 418 (fig. 1726), p. 12, pl. 419 (figs 1727–1729).

?1965 *Bostrychoceras* sp. aff. *indicum* Stol.; Collignon, p. 12, pl. 419 (fig. 1730).

1967 *Eubostrychoceras indopacificum* Matsumoto, p. 333, pl. 18 (fig. 1).

1976 *Didymoceras* (*Didymoceras*) sp. gr. ex. *indicum* (Stoliczka); Klinger, p. 64 (*pars*), pl. 24 (fig. 3) only.

1986 *Nostoceras* (*Eubostrychoceras*) *indopacificum* Matsumoto; Kennedy, p. 101, text-fig. 36.

#### Type

Holotype is the specimen figured in Matsumoto (1967, pl. 18 (fig. 1)) from the Coniacian of Sakurazawa, Fukushima Prefecture, northwest Japan.

#### Material

SAM-PCZ18708 (ex SAS-Z1078), SAM-PCZ17332 (ex 33/li), both from locality 71, KwaZulu, St Lucia Formation, Coniacian I (?II).

#### Description

Both specimens are small and are probably microconchs. Coiling is dextral in SAM-PCZ18708 and sinistral in SAM-PCZ17332. The successive whorls are in close contact, but apparently not impressed into each other.

Ornament consists of predominantly single, slightly rursiradiate ribs—in SAM-PCZ18708 about 40 per whorl and in SAM-PCZ17332 about 70. Constrictions are common and conspicuous, occurring approximately once per half whorl. This results in all the constrictions being slightly offset, one above the other in a line parallel to the axis of coiling.

#### Discussion

Kaplan & Schmid (1988: 52) described the extent of variation in the upper Turonian to possibly basal Coniacian species *E. (E.) saxonicum*, and discussed the difficulty of separating it from allied species such as *E. (E.) indopacificum* and *E. (E.) muramotoi* Matsumoto, 1967. In terms of rib density, closely coiled Turonian–Coniacian species of *Eubostrychoceras* can be arranged from coarsely costate *E. (E.) matsumotoi* Cobban, 1987 with 20 to 30 ribs per whorl, through *E. (E.) indopacificum* with 50 to 55 per whorl, to *E. (E.) saxonicum* with 30 to 80 per whorl. In terms of rib density, our specimens clearly connect with *E. (E.) indopacificum* and *E. (E.) saxonicum*. The spacing of the constrictions is similar to that of *E. (E.) muramotoi* Matsumoto 1967. Our material is best referred to *E. (E.) indopacificum*.

#### Occurrence

Coniacian of Japan, India, Madagascar, and KwaZulu.

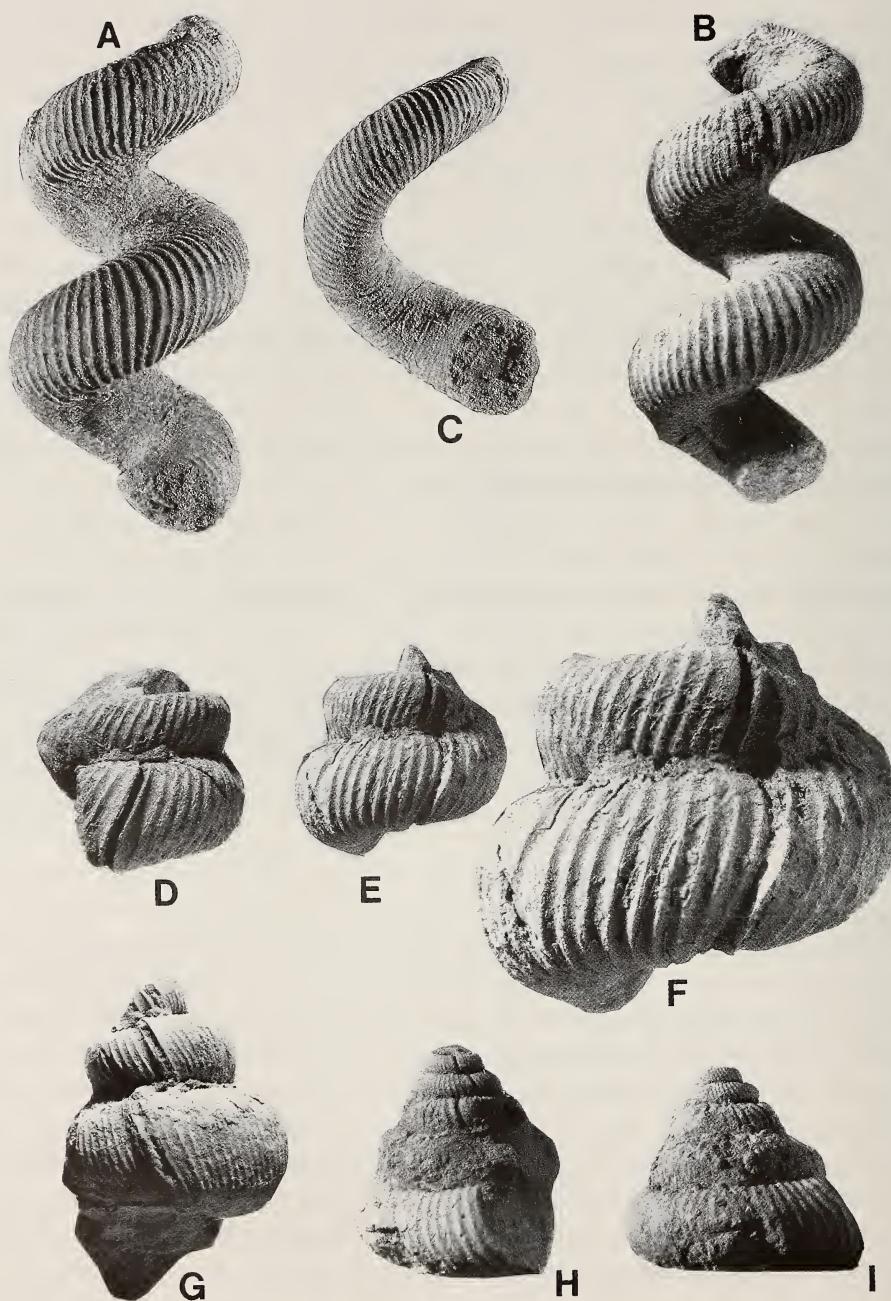


Figure 1

*Eubostrychoceras (Eubostrychoceras) nibelae* sp. nov.

Fig. 1H–I

1976 *Didymoceras (Didymoceras) sp. gr. ex. indicum* (Stoliczka); Klinger, p. 64 (*pars*), pl. 24 (fig. 4) only.

*Type*

Holotype by monotypy is SAM-PCZ17333 (ex A430) from locality 111, KwaZulu, St Lucia Formation, Campanian III.

*Etymology*

Named after the Nibela Peninsula on the northern side of Hell's Gates, which connect Lake St Lucia and False Bay, KwaZulu.

*Description*

Coiling is tight with a distinct zone of impression on the upper surface of the whorls. The apical angle (i.e. angle of the helically coiled part of the shell) is wide, approximately 65°. Ornament consists of about 60 slightly rursiradiate and sinuous ribs and regularly-spaced constrictions; one per whorl, resulting in their being aligned obliquely one above the other on the flanks.

*Discussion*

Even though we have only one specimen, the wide apical angle, tight coiling and regular spacing of the constrictions distinguishes this species from all other species of *E. (Eubostrychoceras)* in KwaZulu. The closest match in terms of ornament and constrictions is *E. (E.) indopacificum*, but that species has a smaller apical angle and is younger (Coniacian).

*Occurrence*

Campanian III of KwaZulu.

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Fig 1. (see facing page). A–C. *Eubostrychoceras (E.) protractum* (Collignon, 1969). A–B. SAM-PCF17331 (ex Collignon Collection) from Gisement 719, km 10 000 de la coupe Ampamba Antsirasira (Belo sur Tsiribihina), Madagascar lower Campanian, Zone of *Menabites boulei* and *Anapachydiscus arrialoorensis*, subzone of *Termierella lenticulare*. C. SAM-PCZ18713 from locality 74, KwaZulu, St Lucia Formation, uppermost Santonian or lower Campanian. D–G. *Eubostrychoceras (E.) indopacificum* Matsumoto, 1967. D–F. SAM-PCZ18708. G. SAM-PCZ17332 (ex H33/1), both from locality 71, KwaZulu, St Lucia Formation, Coniacian III. H–I. *Eubostrychoceras (E.) nibelae* sp. nov., SAM-PCZ17333 (ex A430), the holotype from locality 110, KwaZulu, St Lucia Formation, Campanian II. A–E, H–I  $\times 1$ ; F  $\times 2$ .



Figure 2

A. *Eubostrychoceras (E.) zulu* sp. nov. SAM-PCZ17334 (ex A432), the holotype, from locality 72, KwaZulu, St Lucia Formation, Coniacian II. B. *Eubostrychoceras (E.) otsukai* (Yabe, 1904). NMB-D1065, imprecisely located as 'Die Rooiwalle', but probably the same as locality 74, KwaZulu, St Lucia Formation, uppermost Santonian or basal Campanian. Both  $\times 1$ .

***Eubostrychoceras (Eubostrychoceras) zulu* sp. nov.**  
 Figs 2A, 63F

1976 *Didymoceras (Didymoceras) sp. gr. ex. indicum* (Stoliczka); Klinger, p. 64 (*pars*), pl. 24 (fig. 2) only.

*Type*

Holotype is SAM-PCZ17334 (ex A432) from locality 72, KwaZulu, St Lucia Formation, Coniacian II.

*Etymology*

Named after the geographic region of origin.

*Material*

Paratypes are SAM-PCZ18710 (ex A2278), SAM-PCZ18711 (ex A2272), SAM-PCZ18709 and SAM-PCZ18718, all from locality 72, KwaZulu, St Lucia Formation, Coniacian II.

*Description*

Coiling is in a loose helix with the distance between successive whorls about half the height of the previous whorl. The umbilical width increases with growth, but even at the largest preserved diameter, is still less than half the diameter of the whorls.

SAM-PCZ18709 (Fig. 63F) represents the earliest growth stage available, at a whorl diameter of 5 mm. Here, coiling is already distinctly helical, as in the later stages of growth. None of our specimens has the body chamber preserved, and we do not know if the helical mode of coiling continues right up to the aperture, or whether there is an upward change in direction as is characteristic of the subgenus.

Ornament consists of single, rounded ribs which are most prominent on the flanks and weakest on the dorsum. In the early stages of growth these are nearly radial, but with increasing diameter they become progressively rursiradiate and S-shaped. Prominent constrictions are already present on SAM-PCZ18709 at a whorl height of 6 mm, and occur on the whole phragmocone at a frequency of every 3/4 to 1 whorl.

The suture is complex. The position of the siphuncle is interesting. Instead of following the centre of the flanks, it follows a course nearly perpendicular to the axis of coiling.

*Discussion*

*Eubostrychoceras (E.) zulu* has coiling similar to that of *E. (E.) otsukai* (Yabe, 1904) and *E. (E.) protractum* (Collignon, 1969), but these are younger, Santonian-Campanian with larger umbilical widths and different ribbing.

*Eubostrychoceras (E.) zulu* superficially resembles *E. (E.) japonicum* (Yabe, 1904), which was comprehensively described and figured by Matsumoto (1977: 329, pl. 48 (figs 1-4), pl. 49 (figs 1-3), pl. 50 (figs 1-2), pl. 51 (figs 1-2), pl. 52 (fig. 3)). However, in *E. (E.) japonicum* the early whorls are heterostrophic and with a *Scalarites*-like ornament



Figure 3

A-B. *Eubostrychoceras (E.) otsukai* (Yabe, 1904). SAM-PCZ17335 from locality 74, KwaZulu, St Lucia Formation, uppermost Santonian or basal Campanian. C. *Eubostrychoceras (E.) auriculatum* (Collignon, 1965). SAM-PCF17336 (ex Collignon Collection) from Beantay, Madagascar, Coniacian. Both  $\times 1$ .

(see Tanabe *et al.* (1981: 216, text-fig. 1; pl. 35 (fig. 1a–e)), Okamoto 1988, pl. 7 (fig. 9))—quite unlike those of *E. (E.) zulu*. Here, the earliest known whorls are already coiled in a corkscrew with uniform ribbing and constrictions. We suspect that the earliest part of the shell may have been straight as in *Hyphantoceras (H.) orientale* (Yabe) as figured by Okamoto (1988, pl. 7 (fig. 8)), pointing away from the helix.

#### Occurrence

Coniacian II of KwaZulu.

*Eubostrychoceras (Eubostrychoceras) otsukai* (Yabe, 1904)

Figs 2B, 3A–B, 4

1904	<i>Heteroceras</i> (?) <i>otsukai</i> Yabe, p. 14, pl. 4 (figs 1–2), pl. 6 (fig. 7).
1932	<i>Bostrychoceras Boulei</i> Collignon, p. 40, pl. 9 (fig. 4, 4a).
?1932	<i>Bostrychoceras Condamiyi</i> Collignon, p. 39, pl. 9 (figs 1–2).
1969	<i>Bostrychoceras otsukai</i> (Yabe); Collignon, p. 31, pl. 524 (figs 2066–2068).
1969	<i>Bostrychoceras boulei</i> Coll.; Collignon, p. 34, pl. 525 (figs 2071–2072).

#### Type

Holotype is the specimen figured by Yabe (1904, pl. 4 (fig. 1)) from the Santonian of Kikumezawa, Ikushumbets, Hokkaido.

#### Material

NMB–D1065, imprecisely located as ‘northwestern end of False Bay’, but probably the same as locality 74, Die Rooiwalle, SAM–PCZ17335, SAM–PCZ9550 both from locality 74, KwaZulu, St Lucia Formation, uppermost Santonian or basal Campanian, SAM–PCZ18712 (ex H179/21) from locality 6, KwaZulu, uppermost Santonian or basal Campanian, SAM–PCZ12939 (ex H40/2) from field locality H40, Nyalazi, KwaZulu, St Lucia Formation, Campanian I.

#### Description

The most complete specimen NMB–D1065 (Fig. 2B) is preserved as an internal mould and consists of two and a half continuous whorls. The other specimens each consist of less than a whorl. In NMB–D1065 coiling is dextral in a loose helix with the distance between the successive whorls equal to about the height of the lower whorl. The umbilicus is very narrow and shows little if any increase in width from the early to the later whorls. The whorl section is virtually circular.

Ornament consists of about 36 to 50 slightly S-shaped, sharp-crested prominent ribs, separated by interspaces wider than the ribs themselves. SAM–PCZ18712 (Fig. 4) is the most coarsely ornamented with about 18 ribs per half whorl. On the adapical part of the whorl the ribs show a sudden ‘knick-point’ and, converging, continue in an apertural direction before passing radially, but much weakened over the dorsum. On the abapical part of the whorls the ribs do not show this sudden change in direction and merely weaken



Figure 4

A-C. *Euhostrychoceras (E.) otsukai* (Yabe, 1904). SAM-PCZ18712 (ex H179/21) from locality 6, KwaZulu, St Lucia Formation, uppermost Santonian or basal Campanian.  $\times 2$ .

towards the dorsum. Three prominent constrictions, approximately one per whorl, associated with an abapical flared rib are visible in NMB-D1065.

### Discussion

The loose, corkscrew-like coiling and narrow umbilicus, associated with the distinctive ornament on the venter and adapical shoulder are characteristic of the species as interpreted by Collignon (1969: 31).

Matsumoto (1977: 331) stated that *Eubostrychoceras (E.) otsukai* is difficult to interpret on the basis of the type material, as well as separating it from the older (Turonian) *E. (E.) japonicum*. It is curious that Matsumoto did not discuss Collignon's (1969: 31) interpretation of *E. (E.) otsukai*. Should the Madagascan and KwaZulu material not belong to *E. (E.) otsukai*, we suggest that as first revising authors, the valid name for the material should be *E. (E.) condamyi* as originally described by Collignon (1932: 39, pl. 9 (figs 1–2)).

*Eubostrychoceras (E.) japonicum* has similar loose coiling on the major part of the phragmocone, but the ornament differs from that of *E. (E.) otsukai* as interpreted by Collignon (1969: 31). Ribbing continues virtually radially over the adapical edge instead of changing direction suddenly as in *E. otsukai*. Also, flared ribs occur on the early and late stages of ontogeny in *E. (E.) japonicum*. The Campanian specimen figured by Collignon (1932: 40, pl. 9 (fig. 3,3a)) as *Bostrychoceras japonicus* Yabe certainly does not belong to that species and is probably conspecific with *E. (E.) otsukai*.

*Eubostrychoceras (E.) boulei* Collignon (1932: 40, pl. 9 (fig. 4, 4a); 1969: 34, pl. 525 (figs 2071–2072)) is a similar loosely coiled species, but has a wider umbilicus, equal to twice the whorl width. We suspect that *E. (E.) boulei* is possibly only a looser coiled form of *E. (E.) otsukai*.

*Eubostrychoceras (E.) protractum* Collignon (1969: 31, pl. 524 (figs 2069–2070)) (see also below) is easily distinguished by the much finer and denser ribbing.

### Occurrence

The type material of *E. (E.) otsukai* is dated as Santonian; the Madagascan specimens are abundant (Collignon 1969: 31 mentioned one hundred specimens) in the upper part of the lower Campanian. The KwaZulu material is probably also from the lower Campanian, but may extend down to the uppermost Santonian.

*Eubostrychoceras (Eubostrychoceras) protractum* Collignon, 1969  
Fig. 1A–C

1969      *Bostrychoceras protractum* Collignon, p. 31, pl. 524 (figs 2069–2070).

### Type

Holotype is the specimen figured by Collignon (1969, pl. 524 (fig. 2069)) from the lower Campanian of Gisement 320, Coupe Ampolopoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar.

### Material

SAM-PCZ18713, PCZ18714, PCZ18715, PCZ18716, PCZ18717, all imprecisely located as 'northwestern end of False Bay', probably the equivalent of our locality 74, Die Rooiwalle, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian.

### Description

The ornament is very characteristic, consisting of fine, slightly rursiradiate ribs. These are strongest on the outer flank (venter) and weaken on the adapical and abapical umbilical shoulders. The ribs are typically single, but occasional irregular bifurcating or intercalatory ribs occur. The ribs number about 100 per whorl. Distinct constrictions are visible at all growth stages. In SAM-PCZ18717 two constrictions are present per half whorl.

### Discussion

The loose coiling, dense ribbing and distinct constrictions are characteristic of the species. Our material is identical to that figured by Collignon, and topotype material (Fig. 1A–B).

As far as density of ribbing is concerned, the upper Santonian/lower Campanian loosely coiled *E. (Eubostrychoceras)* species can be arranged from coarsest *E. (E.) elongatum*, through *E. (E.) otsukai* to *E. (E.) protractum* (finest).

*Eubostrychoceras (E.) densicostatum* Matsumoto (1977: 332, pl. 52 (fig. 2)) has a comparable rib density, but the whorls are in contact in later stages of growth.

### Occurrence

Lower Campanian of Madagascar, upper Santonian and/or lower Campanian of KwaZulu.

*Eubostrychoceras (Eubostrychoceras?)* sp.

Fig. 9D–E

### Material

SAM-PCZ18750 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian.

### Description and discussion

A single fragment from this locality differs from all other known heteromorphs from KwaZulu. It consists of part of a helical whorl which passes into a straight shaft with noticeable increase in whorl diameter, associated with a prominent constriction. Ornament consists of single, simple sharp ribs, separated by wide interspaces. No signs of tubercles are visible.

The small size and uncoiled body chamber clearly separates this specimen from all known species of *Eubostrychoceras* in KwaZulu. The absence of tubercles and the upper Santonian or lower Campanian occurrence of this specimen rule out the possibility that this might be a fragment of *Nostoceras*.

*Occurrence*

Upper Santonian or lower Campanian of KwaZulu.

Subgenus *Eubostrychoceras* (*Amapondella*) Klinger & Kennedy, 1997

*Type species*

*Heteroceras amapondense* Van Hoepen, 1921 (1921: 17, pl. 4 (figs 1–2)) by original designation of Klinger & Kennedy (1997: 246).

*Diagnosis*

Earliest whorls apparently helical, tightly coiled, followed by major part of shell which forms a low helix, and ending in an upcurved limb which reaches up to or slightly over the apex of the helical section. Ornament initially consists of simple ribbing only; at a later, variable stage, intercalated flared ribs occur.

*Discussion*

Klinger & Kennedy (1997: 244–246) recently discussed the affinities of the type species of *Eubostrychoceras* (*Amapondella*), *Heteroceras amapondense* and concluded that it was neither a typical *Hyphantoceras* nor a *Madagascarites* as tentatively implied by Klinger's (1976: 71) reference to it as *Hyphantoceras* (*Madagascarites?*) *amapondense*.

*Occurrence*

Upper Santonian of Pondoland, offshore deposits of Natal Coast, KwaZulu, Israel, Austria, France and Mississippi, and lower Campanian of Madagascar and KwaZulu.

*Eubostrychoceras* (*Amapondella*) *amapondense* (Van Hoepen, 1921)

Figs 5, 6, 7A, 8A–D, 9A–C

- 1906 *Heteroceras* sp. Woods, p. 339, pl. 42 (fig. 4).
- 1906 *Heteroceras* sp. Woods, p. 339, pl. 42 (fig. 5).
- 1906 *Hamites* (*Anisoceras*) sp. Woods, p. 340, pl. 44 (fig. 3).
- 1921 *Heteroceras amapondense* Van Hoepen, p. 17, pl. 4 (figs 1–2).
- 1921a *Bostrychoceras?* sp. Spath, p. 255, pl. 24 (fig. 2).
- 1921a *Bostrychoceras?* sp. nov. Spath, p. 252.
- 1969 *Anaklinoceras stephensonii* Collignon, p. 50, pl. 532 (fig. 2096).
- 1969 *Hyphantoceras reussianum* d'Orb; Collignon, p. 38, pl. 527 (figs 2079–2080).
- 1976 *Hyphantoceras* (*Madagascarites?*) *amapondense* (Van Hoepen); Klinger, p. 71, pl. 32 (fig. 5a–b), pl. 33 (figs 2–3), text-fig. 10d–e.
- 1976 *Hyphantoceras* (*Hyphantoceras*) sp. A. Klinger, p. 70, pl. 32 (figs 2–4), pl. 32 (fig. 1).
- 1979 *Hyphantoceras* (*Madagascarites?*) *amapondense* (Van Hoepen); Summesberger, p. 123, pl. 3 (fig. 19), text-fig. 13.
- 1980 *Hyphantoceras* (*Madagascarites?*) *amapondense* (Van Hoepen); Summesberger, p. 277, pl. 1 (fig. 2), text-fig. 3.

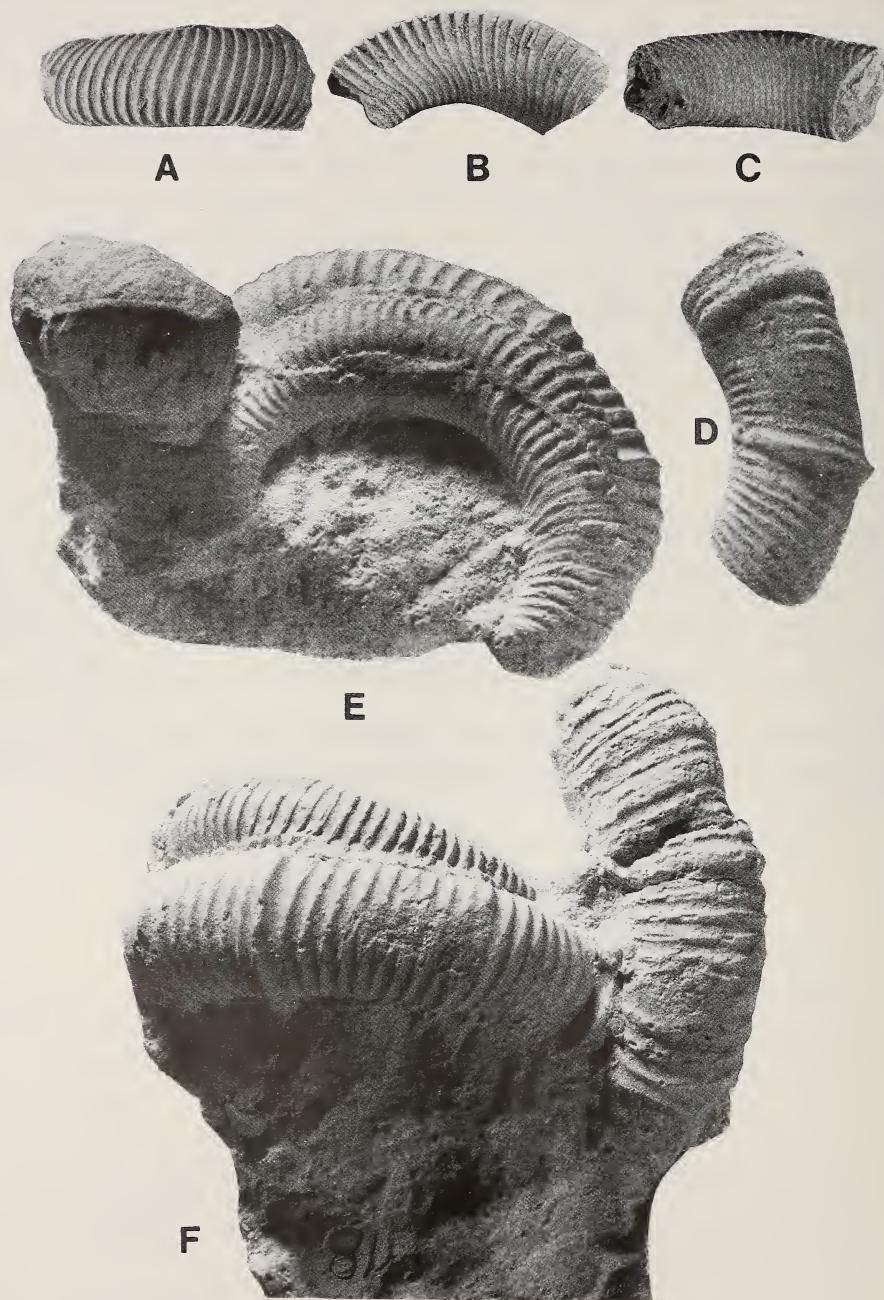


Figure 5

1983 *Hyphantoceras(?) amapondense* (van Hoepen); Lewy, p. 24, figs 1–6.

1985 *Hyphantoceras (?Madagascarites) amapondense* (Van Hoepen); Klinger, p. 6, figs 4i–K.

1987 *Hyphantoceras (?Madagascarites) amapondense* (van Hoepen); Immel, p. 134.

1991a *Hyphantoceras(?) amapondense* (van Hoepen); Kennedy & Cobban, p. 181, fig. 9: 9,10.

1995 *Hyphantoceras(?) amapondense* (Van Hoepen); Kennedy, p. 428, pl. 28 (figs 24–30).

1997 *Eubostrychoceras (Amapondella) amapondense* van Hoepen; Klinger & Kennedy, p. 244, figs 12–14A, 15A–D, 17A–C.

#### Type

Holotype by original designation is the specimen figured by Van Hoepen (1921, pl. 4 (figs 1–2)) in the Transvaal Museum Collections (Fig. 5E–F) from an unspecified horizon at locality 1, Mzamba River Estuary, Pondoland, Eastern Cape Province, Mzamba Formation, Santonian III?.

#### Material

A cast of the holotype, SAM-PCZ18722, from an unknown horizon at locality 1, Pondoland, Eastern Cape Province, Mzamba Formation, Santonian III?, also CGH (= SAM-PCP12882), SAM-PCP6890, SAM-PCP6891, SAM-PCP17368, SAM-13227, SAM-PCZ18729, SAM-PCZ18725, SAM-PCP18724, SAM-PCP18723, SAM-4821, SAM-PCP18726 SAM-PCP18721, SAM-7060, SAM-7061, all also from an unspecified horizon at locality 1; SAM-PCP8277, SAM-6890, SAM-8285, from Bed 7 at locality 1, Santonian III; SAM-PCZ7318, SAM-PCZ7321, SAM-PCZ7328, SAM-PCZ7342, SAM-PCZ17372 (ex Z2071) loose at locality 105, KwaZulu, St Lucia Formation, Santonian III or Campanian I; SAM-PCZ12881 (ex H126E/1), SAM-PCZ18719 from bed 5 at the same locality, Campanian I; SAM-PCZ18730 (ex H125) from locality 107, KwaZulu, St Lucia Formation, Campanian I; SAM-PCZ18727 (ex H77/H1) from locality 75, KwaZulu, St Lucia Formation, Santonian; SAM-PCZ18728 (ex H36/2) from locality 31, KwaZulu, St Lucia Formation, Santonian; SAM-PCF18720, SAM-PCF17338 (ex Collignon Collection) from Madagascar.

#### Description

Coiling is helical in the major part of the shell, forming a low spire with the whorls either just touching or slightly impressed; part of the body chamber curves upward, and over the apex of the helix. Ornament in the early stages consists of single ribs only; in later stages of the phragmocone and body chamber flared ribs occur between normal ribs.

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Fig 5. (see facing page). *Eubostrychoceras (Amapondella) amapondense* (Van Hoepen, 1921). A–C. SAM-PCP18721 from locality 1, the Mzamba Estuary, Eastern Cape Province, Mzamba Formation, upper Santonian or lower Campanian. D. SAM-PCF17338 (ex Collignon Collection) labelled 'Hyphantoceras' from Mitraiky, north of Manimbilo, Madagascar, Santonian. E–F. SAM-PCP18722. Cast of the holotype, Transvaal Museum collections from an unspecified horizon at the type locality of the Mzamba Formation at the Mzamba River Estuary, Eastern Cape Province, upper Santonian or lower Campanian. All  $\times 1$ .

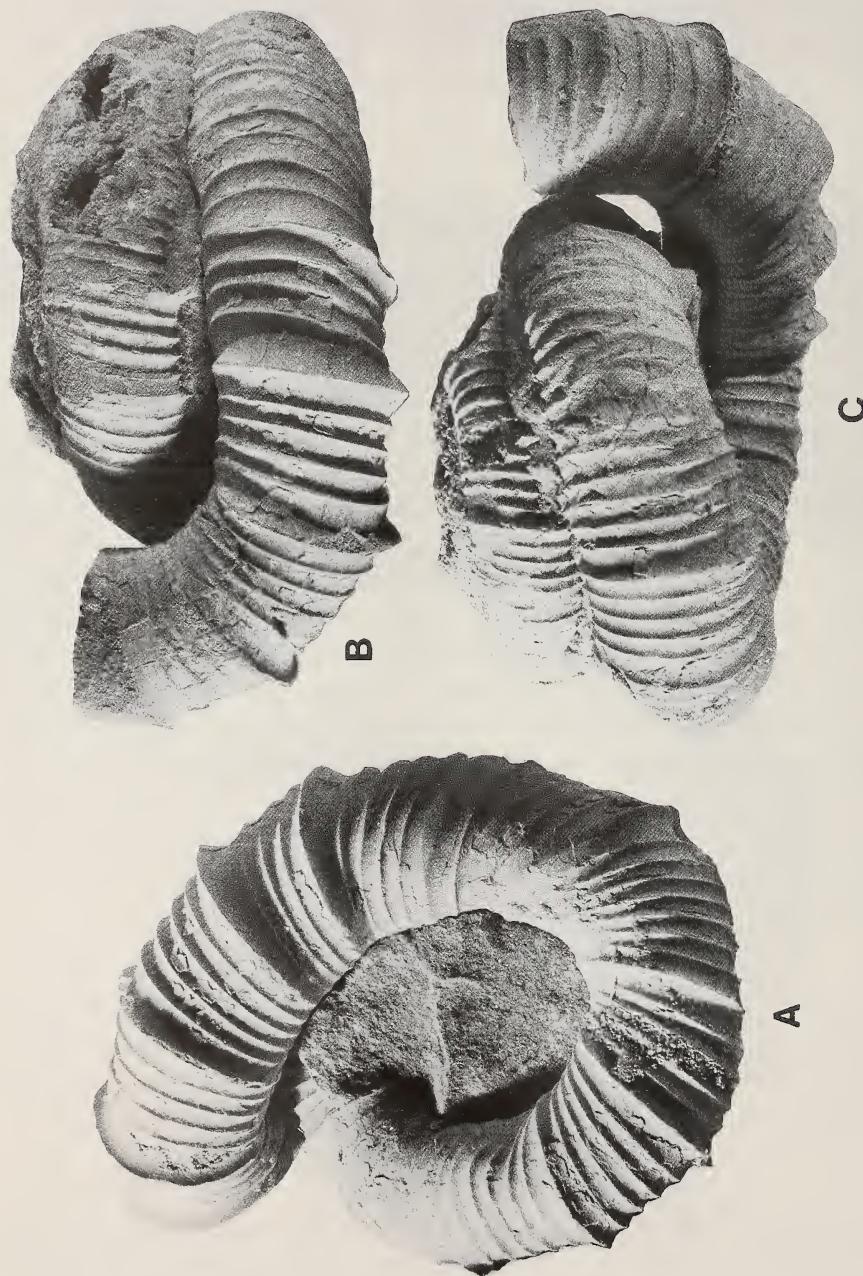


Figure 6

*Eubostrychoceras (Amapondella) amapondense* (Van Hoepen, 1921). SAM-PCZ7328 from locality 105, KwaZulu, St Lucia Formation, Campanian I.  $\times 1$ .

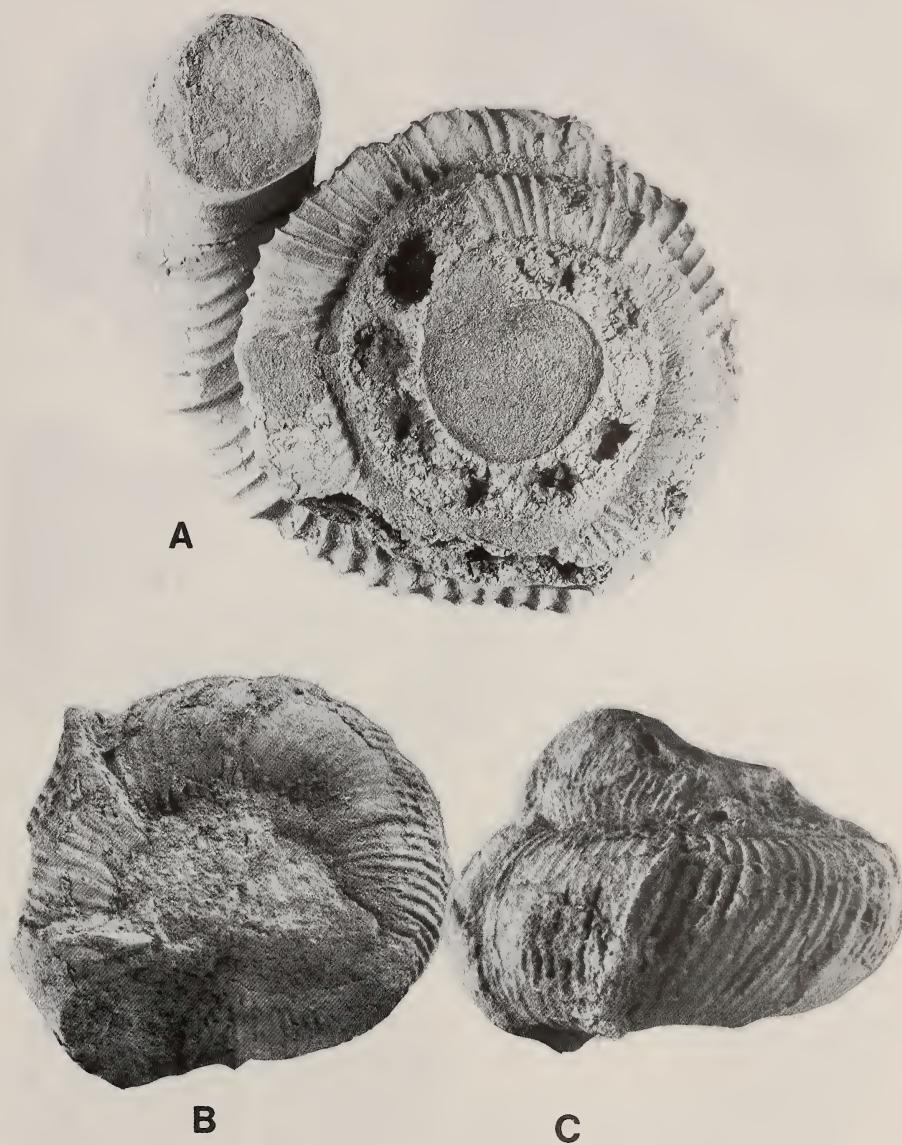


Figure 7

A. *Eubostrychoceras (Amapondella) amapondense* (Van Hoepen, 1921). SAM-PCZ7328 from locality 105, KwaZulu, St Lucia Formation, Campanian I. B-C. *Eubostrychoceras (E.) auriculatum* (Collignon, 1965). SAM-PCF17370 (ex Collignon collection) from Gisement 335, Beantaly (Belo sur Tsiribihina), Madagascar, lower Coniacian. Both  $\times 1$ .

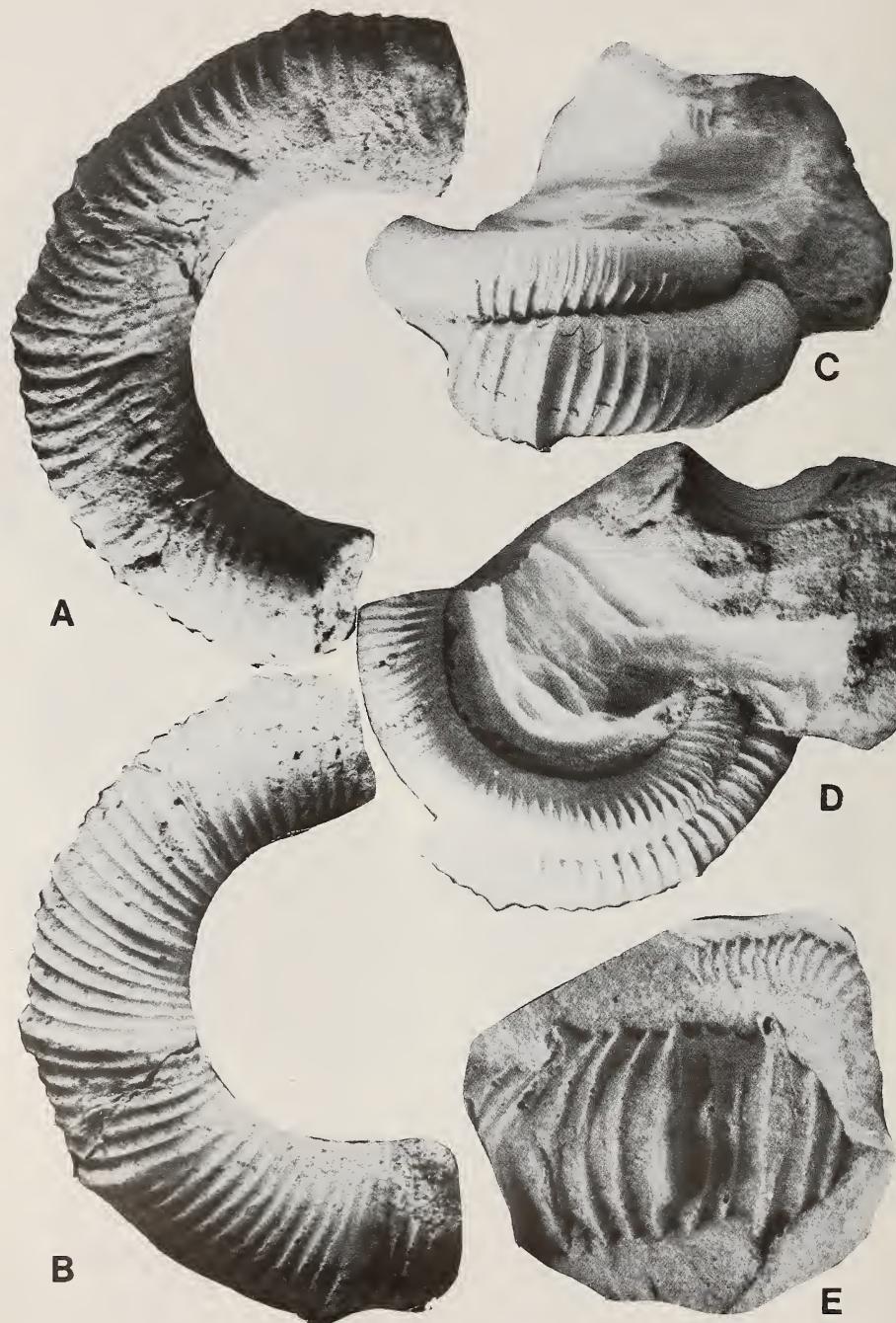


Figure 8

## Discussion

This species is quite variable in overall size, tightness of coiling, and the stage at which flared ribbing first appears. Since Klinger's (1976) description of the species from Pondoland and KwaZulu, and inclusion of the Madagascan *Anaklinoceras? stephensonii* Collignon (1969: 50, pl. 532 (fig. 2096)) in its synonymy, *E. (A.) amapondense* has been recorded from the offshore deposits off the Natal South Coast (Klinger 1985), the upper Santonian of the Gosau Basin of Austria (Summesberger 1979, 1980; Immel 1987) (although Kennedy & Cobban 1991: 182 suggest that it may belong to *Jouaniceras sicardi* (De Grossouvre)), upper Santonian of France (Kennedy 1995), the upper Santonian of Israel (Lewy 1983), and Mississippi (Kennedy & Cobban 1991). We have also seen a specimen from the middle Santonian of Madagascar in the Collignon collection in Dijon.

The description of this latter material, especially that from Israel and additional material from Pondoland and KwaZulu clearly show that *Hyphantoceras* sp. A of Klinger (1976: 32 (figs 2–4), pl. 33 (fig. 1a–b)) is a synonym of *E. (A.) amapondense*. Klinger (1976: 71) admitted that *Hyphantoceras* sp. A and *E. (A.) amapondense* were practically indistinguishable in small fragments, but thought that the former differed on account of the tighter coiling and ovoid whorl section. We agree with Lewy (1983: 25) that these differences are within the range of variation of *E. (A.) amapondense*.

Some of the Campanian Madagascar specimens identified by Collignon (1969: 38, pl. 527 (fig. 2079–2080)) as *Hyphantoceras reussianum* (d'Orbigny, 1850)—a typical Turonian species, are also parts of *E. (A.) amapondense*. But *H. reussianum* in Collignon (1969: 29, 523 (fig. 2064)) is different. According to Matsumoto (1977: 308) it may be an example of *Ainoceras* Matsumoto & Kanie, 1967. An alternative explanation is that it could be a coarsely ribbed *E. (Eubostrychoceras)*—allied perhaps to *E. (E.) junior* (Moberg, 1885). Undescribed specimens labelled as 'Hyphantoceras' (ex Collignon collection) from the Santonian of Mitraiky, Madagascar (Figs 5D, 9A) also belong to *E. (A.) amapondense*.

The specimen from Mkweyane (Umkwelane Hill) described and figured by Spath (1921a: 255, pl. 24 (fig. 2)) as *Bostrychoceras?* sp. ind. also belongs to *E. (A.) amapondense*. It is on the same block of matrix from which *Diaziceras tissotiaeforme* Spath (1921a: 245, pl. 19 (fig. 1a–c)) was extracted. Spath also described several fragments as *Bostrychoceras?* sp. nov., which he considered to be the same as Woods' (1906, pl. 42 (fig. 5a–b)) specimen. The latter is unquestionably *E. (A.) amapondense*, but Spath's

Fig 8. (see facing page). A–D. *Eubostrychoceras (Amapondella) amapondense* (Van Hoepen, 1921). A–B. SAM-PCZ12881 (ex H126E/1) from Bed E at locality 105, KwaZulu, St Lucia Formation, Campanian I. C–D. SAM-PCP12882 (ex CGH) from an unspecified horizon at the type locality of the Mzamba Formation at the Mzamba Estuary, Eastern Cape Province, Mzamba Formation, upper Santonian or lower Campanian. E. *Didymoceras (Eodidymoceras)?* sp. SAM-PCZ12949 (ex SAS-Z2071), latex peel showing apparent hamitid early whorls and part of body chamber with bituberculate, flared ribs. From an unspecified horizon at locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. All  $\times 1$ .

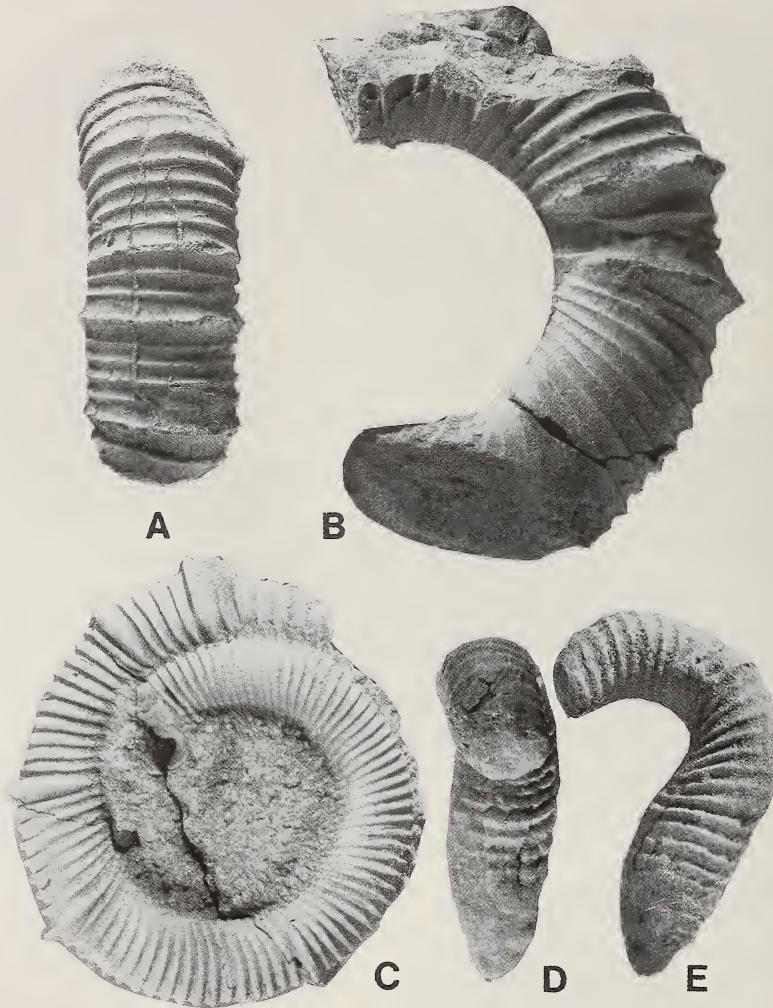


Figure 9

A-C. *Eubostrychoceras (Amapondella) amapondense* (Van Hoepen, 1921). A. SAM-PCF18720 (ex Collignon collection), labelled 'Hyphantoceras' from Gisement 252, Coupe de Bevaho, (Belo sur Tsiribihina), Madagascar, lower Campanian, Zone of *Anapachydiscus wittekindi* and *Eulophoceras jacobi*. B. SAM-PCZ18719 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. C. SAM-PCP6890 from Bed 7 at locality 1, Eastern Cape Province, Mzamba Formation, Santonian III. D-E. *Eubostrychoceras (Eubostrychoceras?)* sp. SAM-PCZ18750 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. All  $\times 1$ .

specimens include parts of straight shafts—e.g. SAM-PCZ18739 and are best referred to *Glyptoxoceras*.

Complete or semi-complete specimens of *E. (A.) amapondense* are rare. However, examination of the holotype and SAM-PCP12882 from Pondoland, SAM-PCZ7328, SAM-PCZ18727 (ex H77/hi) and SAM-PCZ18728 (ex H36/2) from KwaZulu, the holotype of *Anaklinoceras? stephensi* from Madagascar and the specimen from Israel figured by Lewy (1983, figs 1–6) show the range of variation in overall size, tightness of coiling, apical angle of the helix and the stage at which flared ribbing first appears.

The near-complete Israeli specimen and SAM-PCP12882 (CGH) are more or less the same size; yet in the former, flared ribs already occur on the third-last whorl of the helix, whereas the Pondoland specimen only has flared ribbing on the last whorl of the helix. The Israeli specimen also has a lower apical angle. This early onset of flared ribbing corresponds more or less to Klinger's *Hyphantoceras* sp. A., which, as discussed above, is a synonym of *E. (A.) amapondense*. Lewy (1983, figs 4–6) figured the early helical whorls. These show the initial simple ribbing, but with onset of flared ribbing at a diameter of 16 mm. SAM-PCP6890 (Fig. 9C) has simple ribbing up to a diameter of 46 mm; flared ribs only appear beyond that diameter.

Cobban & Scott (1972: 46) compared *Puebloites spiralis* with Woods' (1906: 340, pl. 44 (fig. 3a–d)) *Hamites (Anisoceras)* sp. *Puebloites*, however, is much older (Cenomanian–Turonian) and never develops flared ribbing.

*Ankinatsytes yabei* Collignon (1965: 16, pl. 420 (fig. 1738)) from the lower Coniacian of Madagascar has ornament reminiscent of the later stages of *E. (A.) amapondense* with normal and flared ribs; but the latter are allegedly trituberculate. We can not say whether these two species are related or not.

*Crioceras sertum* Müller & Wollemann (1906: 20, pl. 9 (fig. 3), pl. 10 (figs 1–3)) shows a similar ontogenetic sequence of ornament—simple ribbing on the early whorls followed by intercalated flared ribs on the outer whorls. Unfortunately all the German specimens are crushed, and the complete form of the shell is unknown. It could possibly also be referred to *E. (Amapondella)*. Collignon (1970: 15, pl. 613 (figs 2286–2288)) described and figured a helically coiled heteromorph from the middle Campanian of Madagascar as *Neoglyptoxoceras sertum*. The Madagascan material, however, appears to have regular ribbing throughout, thus differing from the German *Crioceras sertum*. The Madagascan material is here renamed *Neoglyptoxoceras collignonii* nom. nov. The holotype is the specimen figured by Collignon (1970, pl. 613 (fig. 2286)). (See also p. 311).

#### Occurrence

Upper Santonian Pondoland, offshore Natal South Coast, Austria, France and Mississippi, upper Santonian and lower Campanian, KwaZulu and middle Santonian to lower Campanian of Madagascar. Together with the texanitid genera *Submortoniceras* and *Reginaites*, *E. (Amapondella)* is a good indicator of the proximity of the Santonian–Campanian boundary in South Africa.

Genus *Nostoceras* Hyatt, 1894*Type species*

*Nostoceras stantoni retrorsum* Hyatt (1894: 570) by the original designation of Hyatt (1894: 569).

*Diagnosis*

The major part of the phragmocone is coiled in a tight helix. Coiling changes in the later part of the phragmocone and body chamber. Ornament generally consists of two rows of tubercles at some stage; in some forms irregularly developed.

*Discussion*

In most *Nostoceras* (*Nostoceras*) species the body chamber forms a distinct U-shaped loop suspended below the base of the preceding spire, with the aperture often very close to the latter. *N. (N.) liratum* Kennedy 1992b is an exception. Here, the body chamber curves upwards, in contact with the helix. This is reminiscent of *E. (Eubostrychoceras)*, or possibly transitional to *N. (Anaklinoceras)* Stephenson, 1941 (type species *Anaklinoceras reflexum* Stephenson, 1941). In *Nostoceras* (*Anaklinoceras*) the body chamber curves upwards and over the apex of the helix and the shells are generally small. In *Nostoceras* (*Planostoceras*) Lewy, 1967 (type species *Planostoceras rehavami* Lewy, 1967) the body chamber forms a hook at right angles to the axis of coiling of the helix and parallel to the base of the latter. In *Nostoceras* (*Bostrychoceras*) the body chamber also forms a loop suspended below the base of the spire as in *Nostoceras* s.s., but is generally larger, and with irregular tuberculation. In *N. (Pravitoceras)* Yabe, 1902 (type species *Pravitoceras sigmoidale* Yabe, 1902) the terminal hook is in the same plane as the predominantly planispiral phragmocone and is C-shaped, involving a 180° torsion of the shell.

*Occurrence*

Campanian to Maastrichtian.

Subgenus *Nostoceras* (*Nostoceras*) Hyatt, 1894*Type species*

*Nostoceras stantoni retrorsum* Hyatt (1894: 570) by original designation of Hyatt (1894: 569).

*Diagnosis*

The major part of the phragmocone consists of a closely coiled helix, either dextral or sinistral, generally with an acute apical angle, followed by a U-shaped, retroversal body chamber hook which brings the aperture to a position just below the base of the helical stage. Ornament consists of ribs with one or two rows of tubercles; some have no tubercles at all.

### Occurrence

Upper Campanian and Maastrichtian. *Nostoceras* (*Nostoceras*) is best known from North America (Gulf Coast, Atlantic Sea Board and Western Interior), but has also been reported from Colombia (in Cobban 1974: 8), Peru, Argentina, Angola, Nigeria, Libya, Egypt, Israel, Madagascar, KwaZulu, and various regions in Europe including England, Spain, France, Belgium, The Netherlands, Italy, Poland, Ukraine, Austria, Bulgaria, and Russia; and Australia, India and Japan.

#### *Nostoceras* (*Nostoceras*) *subangulatum* Spath, 1921

Fig. 10A

1921a *Nostoceras?* *subangulatum* Spath, p. 250, pl. 22 (fig. 3a–c).

### Type

Holotype by monotypy is SAM-PCZ18731 from east of the Railway at Riverview Halt, KwaZulu, St Lucia Formation, probably Campanian.

### Discussion

No additional specimens of this species have been found and the holotype is here figured (Fig. 10A) for comparison with the holotype of *N. (N.) natalense* which was recorded from the same locality. The ornament of the two species is broadly comparable; both have a large row of tubercles situated just above midflank and a second row at the base of the spire, just visible above the suture between the whorls. The whorl section in *N. (N.) natalense* is more angular, and the apical angle is much larger, resulting in a low, squat spire. In contrast, *N. (N.) subangulatum* has a rounded whorl section and a much smaller apical angle, resulting in a shell shape reminiscent of the turrilitid genus *Mariella* Nowak, 1916 as was also noted by Spath (1921a: 252).

### Occurrence

Probably Campanian, KwaZulu.

#### *Nostoceras* (*Nostoceras*) *natalense* Spath, 1921

Figs 10B–D, 11–12

1921a *Nostoceras?* *natalense* Spath, p. 248, pl. 22 (fig. 2a–b).  
 ?1931 *Turrilites* (*Bostrychoceras*) *Schloenbachi* Favre; Basse, p. 19, pl. 2 (figs 11–15).  
 1965 *Nostoceras(?) obtusum* Howarth, p. 384, pl. 10 (fig. 2), text-fig. 17.  
 ?1971 *Nostoceras obtusum* Howarth; Collignon, p. 9, pl. 643 (fig. 2375).  
 ?1971 *Nostoceras hyatti* Steph.; Collignon, p. 8, pl. 643 (fig. 2371).  
 1976 *Didymoceras* (*D.*) *natalense* (Spath); Klinger, p. 68, pl. 30 (fig. 3), pl. 31 (figs 1–3), pl. 32 (fig. 1).

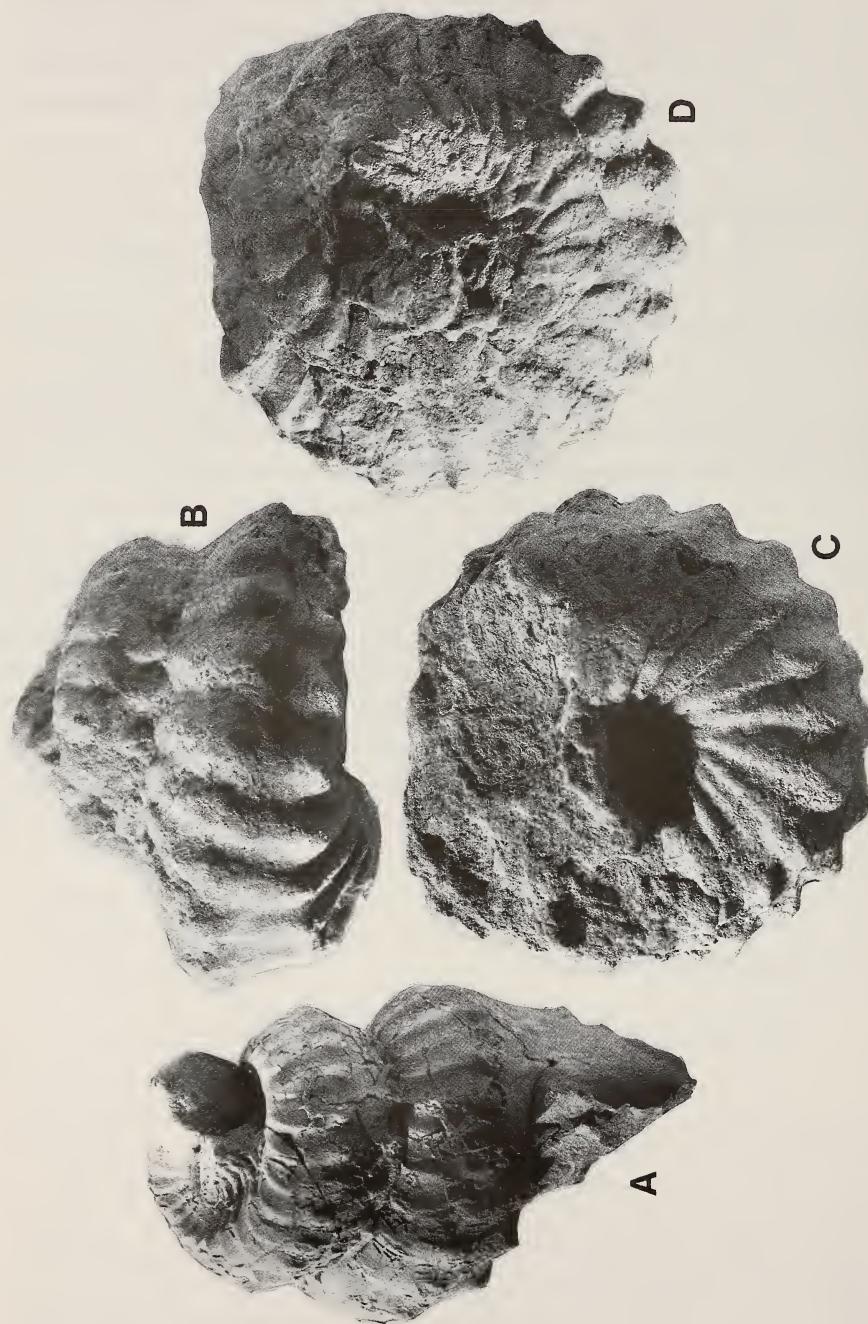


Figure 10

A. *Nostoceras (Nostoceras) subangulatum* Spath, 1921. SAM-PCZ18731, the holotype. B-D. *Nostoceras (Nostoceras) natalense* Spath, 1921. SAM-PCZ18732, the holotype. Both from east of the Railway at Riverview Halt, KwaZulu, St Lucia Formation, probably upper Campanian. Both  $\times 1$ .

### Type

Holotype by monotypy is SAM-PCZ18732 from east of Riverview Railway Halt, KwaZulu, St Lucia Formation, probably Campanian.

### Material

SAM-PCZ18733, SAM-PCZ18734 from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAM-PCZ18736 (ex Z2270) and SAM-PCZ18735 (ex H106) from locality 117, KwaZulu, St Lucia Formation, Maastrichtian a, SAM-PCZ18737 (ex H116/2) from locality 120, KwaZulu, St Lucia Formation, Maastrichtian a.

### Description

Apart from SAM-PCZ18734 (Fig. 11F), no further material has been found since Klinger's (1976) description. The five available specimens show considerable variation. At one end of the scale is a coarsely ornamented form with an apical angle of about 70° as in the holotype (Fig. 10B-D). The ribs on the adapical part of the whorls are broad and strong and incipiently looped in the early whorls. They are connected to large tubercles situated above mid-flank, then weaken on the flank before connecting to a smaller, abaperturally displaced row of smaller tubercles visible just above the whorl suture. The ribs continue over the base of the spire in a prorsiradiate fashion, narrowing towards, and continuing over the whole of the umbilical wall.

The other end of the scale is typified by SAM-PCZ18736 (Fig. 11A) with a wide apical angle of about 130°. Here the adapical part of the whorl is ornamented by much finer ribs and these connect in unequally strong pairs to the upper row of tubercles, which are situated in the whorl suture.

Specimens such as SAM-PCZ18734 (Fig. 11F) and SAM-PCZ18737 (Fig. 11C-E) connect these two extremes of variation. In both, the ribbing is coarser than in SAM-PCZ18736 but still distinctly looped on the upper and lower parts of the whorls. SAM-PCZ18735 (Fig. 11B) consists of the last part of the helix and the retroversal body chamber. A single constriction is present in SAM-PCZ18737 (Fig. 11C-E).

### Discussion

Klinger (1976: 68) regarded the Angolan *N. (N.) obtusum* (Howarth 1965: 384, pl. 10 (fig. 2), text-fig. 17) as a synonym of *N. (N.) natalense*. When compared with the holotype, Howarth's (1965: 384) reasons for maintaining them separate—e.g. large tubercle, bold ribs and smaller umbilicus—seem reasonable. However, SAM-PCZ18734 (Fig. 11F) has an apical angle, open umbilicus and rib density indistinguishable from the holotype of *N. (N.) obtusum*, and we consider *N. (N.) natalense* to be a senior synonym of *N. (N.) obtusum*.

All the specimens described by Basse (1931: 19, pl. 2 (figs 11-15)) as *Turrilites (Bostrychoceras) schloenbachi* are smaller than our smallest specimen. They definitely do not belong to Favre's (1869) *N. (N.) schloenbachi* (see Kennedy & Summesberger 1987: 30-31 for a review of that species). The largest of Basse's specimens (1931, pl. 2 (fig. 15)), however, is very similar to SAM-PCZ18737 (Fig. 11C-E). The impression of

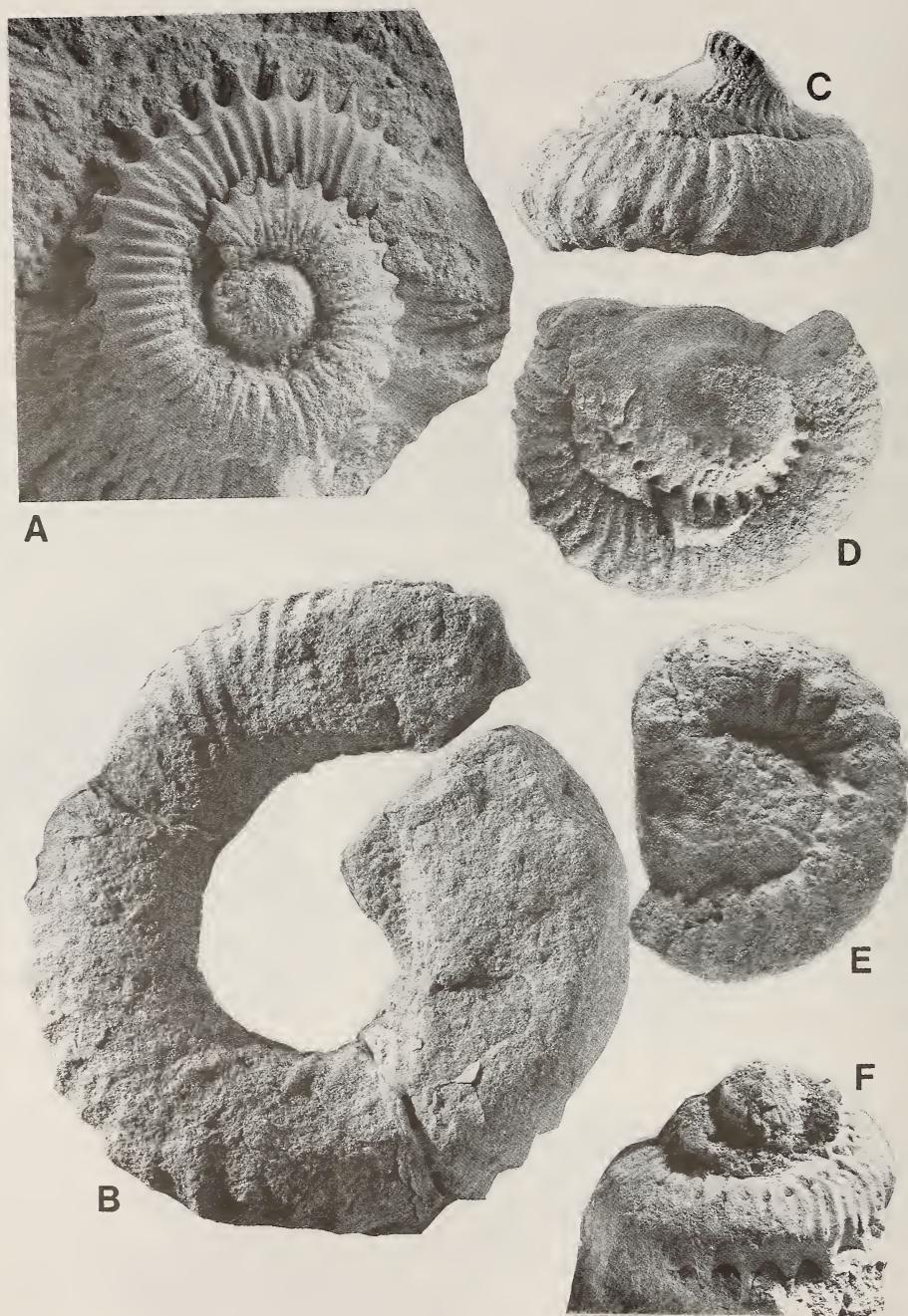


Figure 11



Figure 12

*Nostoceras (Nostoceras) natalense* Spath, 1921. SAM-PCZ18733 (ex 113). A-B. Complete specimen. C-E. Part of outer whorl removed. From locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b. Both  $\times 1$ .

Fig. 11. (see facing page). *Nostoceras (Nostoceras) natalense* Spath, 1921. A. SAM-PCZ18736 (ex Z2270) from locality 117, KwaZulu. Specimen with distinct siphonal spines and bifurcating ribbing on the adapical side. B. SAM-PCZ18735 (ex H106) part of a recurved body chamber from the same locality as A. C-E. SAM-PCZ18737 (ex H116/2) from locality 120, KwaZulu. F. SAM-PCZ18734 from locality 113, specimen showing distinct abapical spines. All from the St Lucia Formation, Maastrichtian a or b. All  $\times 1$ .

an earlier whorl on this specimen shows fine ornament comparable to that of Basse's material.

The specimens figured by Collignon (1971: 13, pl. 644 (figs 2385–2386)) as *Didymoceras schloenbachi* could also possibly be included in *N. (N.) natalense*, but they are too small for definite allocation. At any rate, they also do not belong to Favre's species.

*Nostoceras obtusum* Howarth in Collignon (1971: 9, pl. 643 (fig. 2375)) from the lower Maastrichtian of Mont Ambohitrombe, Madagascar is very similar to the KwaZulu specimen SAM-PCZ18737 (Fig. 11C–E) and is also tentatively referred to *N. (N.) natalense*.

Another specimen figured by Collignon (1971: 8, pl. 643 (fig. 2371)) as *Nostoceras hyatti* Stephenson is possibly also a *N. (N.) natalense*, comparable to the finely ribbed forms, e.g. SAM-PCZ12942 (Fig. 11A).

Our finer ribbed specimen, SAM-PCZ18736 (Fig. 11A) resembles some *Nostoceras (N.) alternatum* (Tuomey, 1851) as figured by Cobban (1974: 86, figs 1w–rr, 5) and Cobban & Kennedy (1991: E3, pl. 2 (figs 5–27)). This species has a similar prominently pointed row of upper tubercles connected by looped ribs on the adapical edge. Generally, however, it seems to have a larger apical angle (45–90°) and a higher spire—compare e.g. Cobban's (1974, fig. 5) restoration of *N. (N.) alternatum* with SAM-PCZ18736 (Fig. 11A). Some specimens, e.g. Cobban & Kennedy (1991, pl. 2 (figs 12–13)) with a wide apical angle are indistinguishable from SAM-PCZ18736. The similarity between *N. (N.) alternatum* and *N. (N.) obtusum*, the latter here regarded as a synonym of *N. (N.) natalense*, was also noted by Cobban & Kennedy (1991: E3) and Cobban (1974: 87). Given more material, *N. (N.) natalense* and *N. (N.) alternatum* may eventually turn out to be the same, or possibly only different subspecies.

Küchler & Odin (2001: 509) commented on the similarities between *Nostoceras (N.) obtusum* and *N. (N.) schloenbachi* (Favre, 1869), but separated the latter on account of the more rounded whorl section and coarser ribs and/or much coarser tubercles.

#### *Occurrence*

Maastrichtian a or b KwaZulu, lower Maastrichtian Madagascar, Campanian/Maastrichtian, Angola, uppermost Campanian of Tercis, France (as *N. (?D.) obtusum* (Küchler & Odin 2001: 507)).

#### Subgenus *Nostoceras (Bostrychoceras)* Hyatt, 1900

##### *Type species*

*Turrilites polyplocus* Roemer (1841: 92, pl. 14 (figs 1–2)), by original designation of Hyatt (1900: 588).

##### *Diagnosis*

Coiling helical, initially ornamented by fine ribs and two rows of tubercles; later tuberculation may become irregular or disappear completely. Body chamber forms distinct loop below the spire.

### Discussion

Virtually all the species that had originally been referred to *Bostrychoceras* have now been placed in *Eubostrychoceras*. Simply put, tight, helically coiled specimens with tubercles at some stage of their ontogeny are referred to *Nostoceras* (*Bostrychoceras*), whereas those predominantly without tubercles are referred to *Eubostrychoceras* (*Eubostrychoceras*). Kennedy (1986) examined several specimens of the type species of *N. (Bostrychoceras)* and illustrated the extreme degree of variation, thus eliminating the need for the various names created by Wiedmann (1962), Blaszkiewicz (1980) and recently Küchler (2000).

### Occurrence

Upper Campanian and lower Maastrichtian, Europe, Texas and Angola.

*Nostoceras (Bostrychoceras) sanctaeluciense* Klinger, 1976

Figs 13–40, 47D

?1909 *Anisoceras notabile* Whiteaves sp.; Kilian & Reboul, p. 15 (*par*), pl. 5?, pl. 6 (fig. 1 only).  
 1976 *Didymoceras (Didymoceras) depressum* (Wiedmann) *sanctaeluciense* Klinger, p. 65, pl. 25–28, pl. 29 (figs 1–3), pl. 30 (figs 1–2), text-figs 8f–h.

### Type

Holotype (Figs 13–16) by original designation of Klinger (1976) is SAS-Z762 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b.

### Material

In addition to the original material in the collections of the Council for Geosciences we have numerous specimens from the following localities: SAS-Z2251, SAM-PCZ9028, SAM-PCZ9079, SAM-PCZ9328, SAM-PCZ9334, SAM-PCZ9339, SAM-PCZ10494 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAM-PCZ9329, SAM-PCZ9335, SAM-PCZ9340, SAM-PCZ9342, SAM-PCZ9343, SAM-PCZ17341 (ex H116/7), SAM-PCZ17349 (ex H115/15) SAM-PCZ17350, (ex 115/13) from locality 120, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAM-PCZ10489, SAM-PCZ10490, SAM-PCZ10493, SAM-PCZ10497, SAM-PCZ10500, SAM-PCZ10501, SAM-PCZ10502, SAM-PCZ10505–10507, from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAS-A2009, SAM-PCZ7907, SAM-PCZ9330, SAM-PCZ9331, SAM-PCZ9339, SAM-PCZ9431, SAM-PCZ10495, SAM-PCZ10496, SAM-PCZ10498 (ex A2016), SAM-PCZ10499 from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b; SAM-PCZ7902, SAM-PCZ7927, SAM-PCZ10504, SAM-PCZ10606, SAM-PCZ17343–17346, SAM-PCZ17349, unlocalized from 'The Coves', localities 118–120, KwaZulu, St Lucia Formation, Maastrichtian a or b.

### Diagnosis

Relatively large; low-spired phragmocone, ornamented by 100 to 130 ribs per whorl,



Figure 13

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). Stipple drawing by Samantha Black of the holotype, SAS-Z762 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 0.7$

siphonal and abapical tubercles at some stage; the former disappear at larger diameters. Retroversal body chamber suspended below spire and ornamented irregularly by one or two rows of tubercles.

#### Description

Klinger (1976) described the species in detail, noting the variation in ornamentation on the phragmocone and on the body chamber. The new material includes specimens showing parts of the very early ontogenetic stage and others showing a wide range in overall size and variation in coiling of the phragmocone as well as the body chamber.

The earliest ontogenetic stage is shown in SAM-PCZ10490a, b (Fig. 17A, C), part and counterpart, consisting of four complete whorls. Coiling is very shallow, nearly

planispiral. On the innermost whorl, 32 single, sharp ribs occur. On the second whorl, at a spiral diameter of *c.* 18 mm, spinose siphonal tubercles appear in the umbilical suture, either from single or from paired ribs—their tips resting on the adapical shoulder of the succeeding whorl. Distinct but small tubercles also occur on the inner abapical edge of the third whorl; here rib density has increased to about 80. On the outer whorl, rib density is about 100 to 120. The majority of ribs are single, but some are bifurcate on the inner third of the adapical edge.

Another specimen, SAM-PCZ10489a and b, part and counterpart (Figs 17B, 18B) also shows the early ontogenetic stage. Here, distinct abapical tubercles are visible at a spiral diameter of 25–30 mm. Three to four single ribs occur between these tubercles. In SAM-PCZ10499 (Fig. 19A–B) impressions of siphonal tubercles are still visible at a spiral diameter of 65 mm. On the next whorl, at a diameter of 95 mm, the siphonal tubercles have disappeared, but abapical tubercles are well developed. In SAM-PCZ10495 (Fig. 20) the outermost whorl shows distinct impressions of siphonal tubercles up to a diameter of about 80 mm, after which they disappear—thus confirming Klinger's (1976: 66) observations that siphonal tubercles only persist up to a maximum diameter of about 100 mm.

On internal moulds, ribbing is generally thin and thread-like on the phragmocone. In the original condition, however, the ribs were blade-like with rounded extremities, separated by wider interspaces. These interspaces are in-filled with calcitic matrix. When extracting specimens from the matrix, the layer consisting of the high ribs and interspace matrix usually detaches from the rest of the shell, resulting in a low-relief internal mould. In some specimens, e.g. SAM-PCZ10498 (Fig. 21B) and SAM-PCZ10503, part of the original high-crested ribbing is still preserved.

During ontogeny, the whorl section on the phragmocone changes from depressed (adapical-abapical) to rounded to distinctly laterally (dorsal-siphonal) compressed. Coiling in the phragmocone is both sinistral and dextral. In most specimens the apical angle is very wide, of the order of 120 to 140 degrees e.g. the holotype, SAS-Z762 (Figs 13–16), SAM-PCZ17341 (Fig. 21A), SAM-PCZ10494 (Fig. 22A), etc., but in some specimens, e.g. SAM-PCZ7927 (Fig. 22B), SAM-PCZ17343 (Fig. 22C), SAM-PCZ10493 (Fig. 22D), SAM-PCZ10506 (Fig. 23) and SAM-PCZ17352 (Fig. 47D), the spire is turreted with an acute apical angle of 60 degrees.

The body chamber occupies approximately the last third to quarter (or even less) of a whorl of the spirally coiled section before it breaks away to form a retroversal loop. The whorl section of the body chamber in the spiral section is very characteristic in being high, laterally compressed and in having a distinct adapical zone of impression. The uncoiled section of the body chamber recurses, forming an angle of between 60 and 90 degrees with the base of the spire, and ends very close to the latter. The aperture is preserved in several specimens, e.g. SAM-PCZ10499, SAM-PCZ9328, SAM-PCZ10500 (Fig. 24) SAM-PCZ7902 (Fig. 25A), SAM-PCZ9336, SAM-PCZ10501 (Fig. 26) and SAM-PCZ10506, first forming a slight constriction and then a simple flare. Ornament on the body chamber is quite irregular, consisting of one or two rows of tubercles which are much larger than those of the phragmocone. There is usually a non-tuberculate interval



Figure 14

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). Apical view of the holotype, SAS-Z762 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 0.7$ .

between the last occurrence of tubercles on the spiral section, and the first appearance of tubercles on the body chamber. The suture line is extremely complex and interdigitated.

The species shows an extreme variation in size. This is very obvious by the different sizes of adult specimens with complete, recurved body chambers. In the smallest adult, SAM-PCZ9328 (Figs 29-30), the body chamber detaches itself at a whorl height (adapical-abapical diameter) of 40 mm, whereas the largest, SAM-PCZ17346 (Fig. 31 A-B) uncoils at a height of 85 mm. Other specimens uncoil at intermediate whorl heights:

SAM-PCZ10499-42 mm

SAM-PCZ10504—c. 50 mm

SAM-PCZ10506-55 mm

Holotype—c. 60 mm

SAM-PCZ10505-68 mm.

It is tempting to ascribe the variation in size at which maturity is attained to dimorphism—the small specimens are microconchs and the large ones macroconchs.



Figure 15

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAS-Z762, the holotype from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 0.8$ .

However, as the dimensions indicate, there seems to be a nearly continuous growth series from smallest to largest. If this size difference is indeed due to dimorphism, there is a large degree of overlap in size between microconchs and macroconchs. There are, however, other differences between the small and large specimens. In the smallest specimens, the body chamber occupies very little of the spiral part of the shell. More important, perhaps, is the fact that the retroversal loop is suspended perpendicularly below the base of the

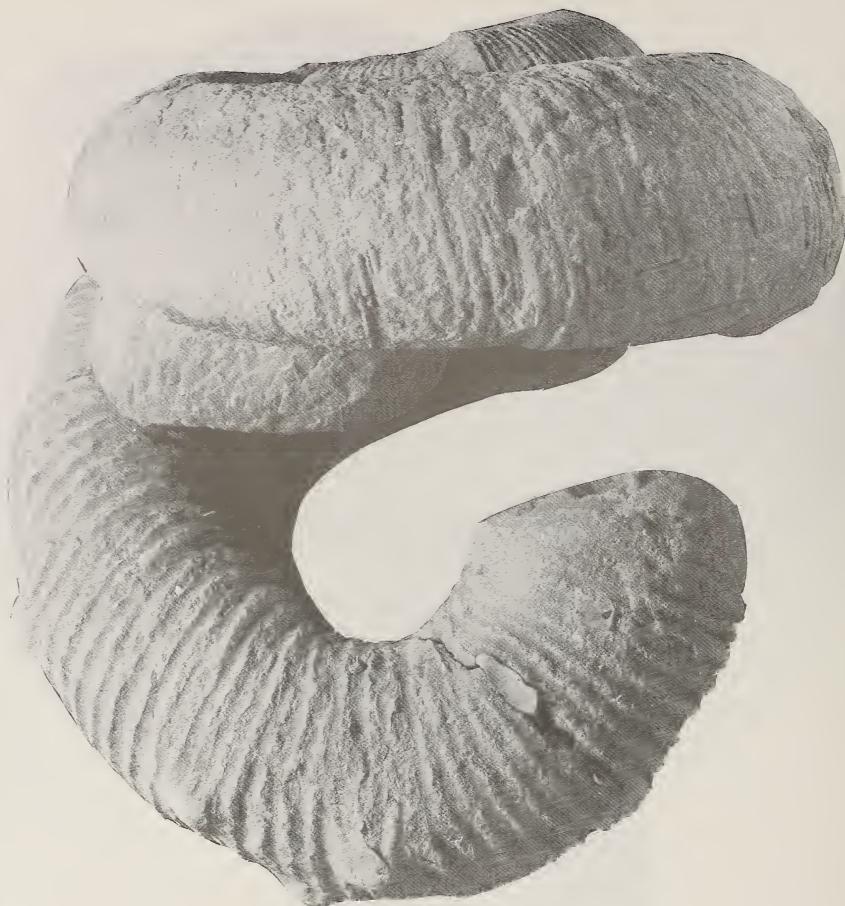


Figure 16

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAS-Z762, the holotype from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 0.7$ .

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Fig. 17. (see facing page). *Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). A, C. SAM-PCZ10490a, b, part and counterpart of the very early helical whorls. Note the very early onset of helical coiling and apparent absence of irregularly coiled early stage. From locality 125, KwaZulu. B. SAM-PCZ10489. Note the development of large, lateral spines on thickened ribs. From locality 119, KwaZulu. D. SAM-PCZ10496. Ventral view of part of phragmocone showing ventral tubercles. From locality 113, KwaZulu. All from the St Lucia Formation, Maastrichtian a or b. All  $\times 1$ .

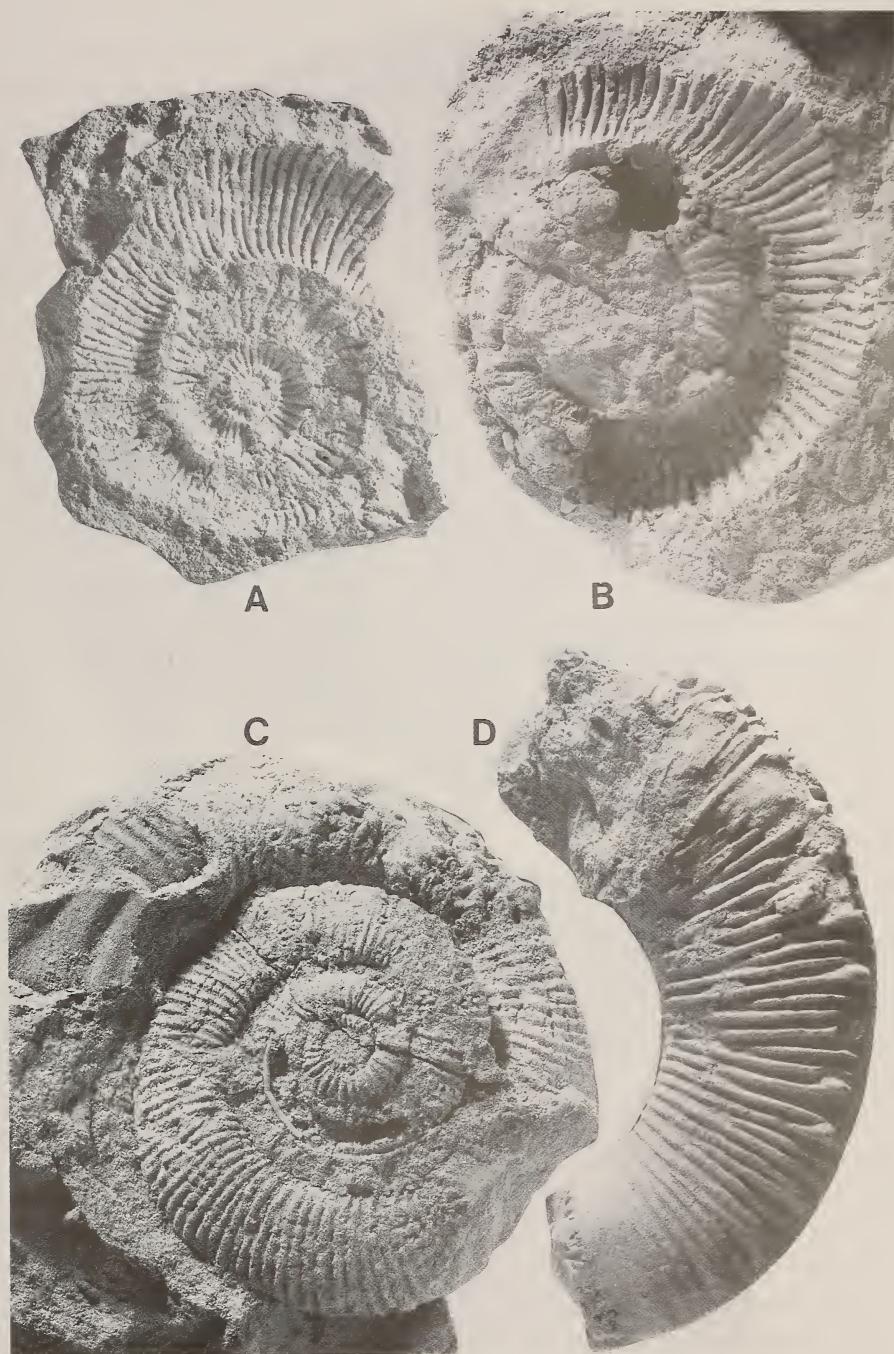


Figure 17

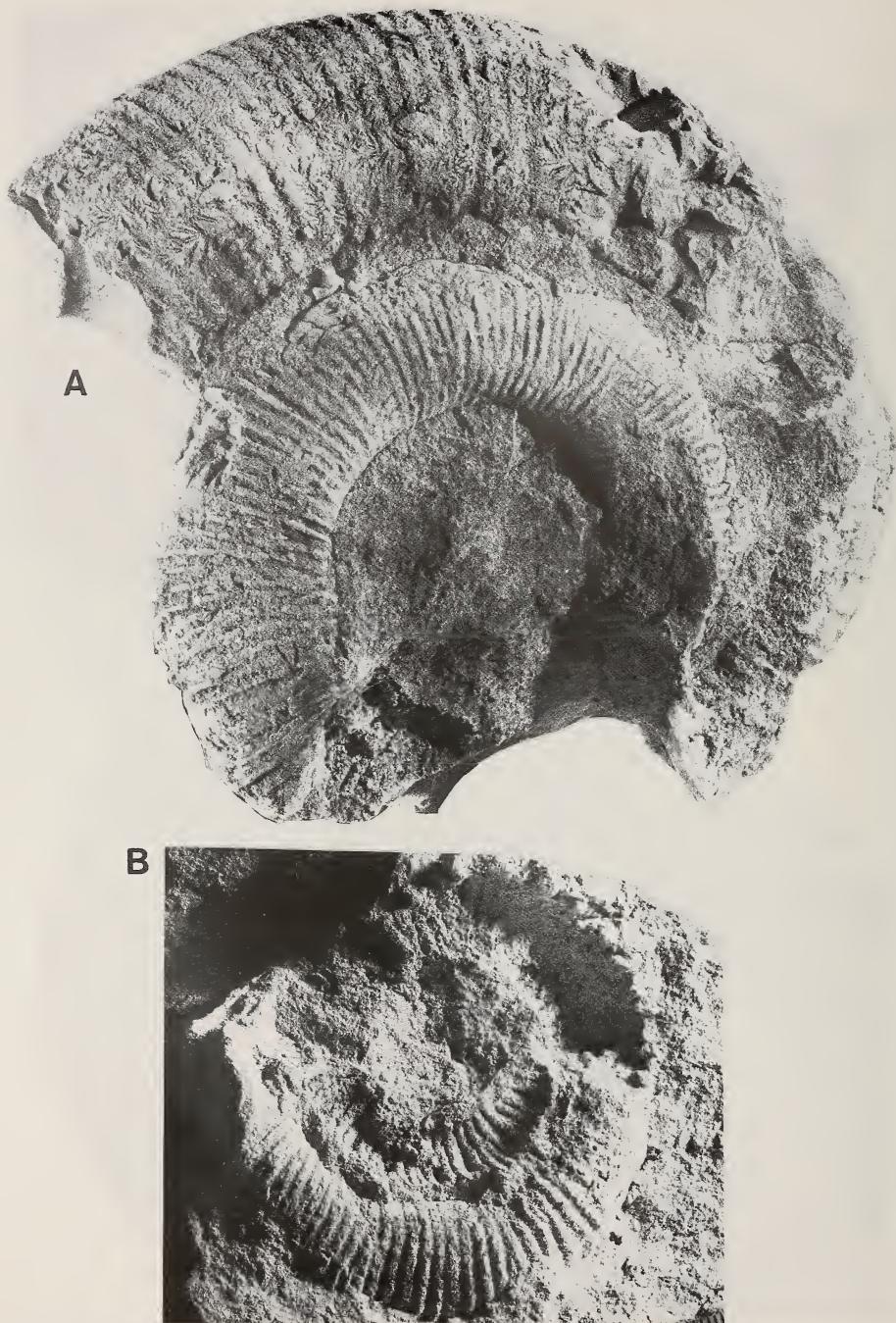


Figure 18

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). A. SAM-PCZ7907. B. SAM-PCZ10489, impression and internal mould of early ontogeny. Both from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b. Both  $\times 1$ .

spire. In contrast, in the large specimens, the body chamber may occupy up to a third of the spiral section, and the retroversal loop forms an angle of about 60 to 70 degrees with the base of the spire.

The differences in size, length of the body chamber and attitude of the retroversal loop suggest, but can not prove, that these variations are due to dimorphism. Another possible explanation is that the differences may be an adaptation to assist in orientation and buoyancy control in the adult stage.

### Discussion

When Klinger (1976) first described this species, he was influenced by Wiedmann's (1962) analysis of northern German specimens of *Nostoceras* (*Bostrychoceras*) *polyplolum* (Roemer, 1841). One or possibly two of Schlüter's specimens of this species (1876, pl. 34 (figs 2–3), ?pl. 34 (figs 4–5)) with a wide apical angle and fewer whorls in the spire were referred by Wiedmann (1962: 199 footnote) to a new species, *Cirroceras* *depressum*. Kennedy (1986) has examined the German collections of *N. (Bostrychoceras) polyplolum* and noted the wide range of variation. It is a typically upper Campanian species, restricted mainly to Europe, but also occurs in Texas (as *Bostrychoceras secoense*) (Young, 1963: 42, pl. 3 (figs 1–5), pl. 4 (figs 4, 8), text-fig. 7s) and Mexico. The KwaZulu material occurs in the lower Maastrichtian, and is unrelated to *N. (Bostrychoceras) polyplolum* as Kennedy (1986: 97) has correctly pointed out.

We were initially inclined to refer this species to the genus *Didymoceras*. The latter, however, has distinct irregular early whorls, and is generally loosely coiled in the later stages. Consequently, we would rather place the species in the subgenus *N. (Bostrychoceras)*.

The specimens figured by Kilian & Reboul (1909, p. 15 (pars), pl. 5, 6 (fig. 1 only)) as *Anisoceras notabile* Whiteaves, 1879, resembles *N. (Bostrychoceras) sanctaeluciense*, but without having seen the actual material, we are uncertain whether they are the same species.

Unfortunately, the Madagascan Maastrichtian heteromorphs are mostly poorly preserved and incomplete. Klinger (1976: 67) suggested that *Nostoceras stantoni serratum* Collignon (1971: 12, pl. 644 (fig. 2383)) may be conspecific. Unfortunately this species is based on half a juvenile whorl and its relation to *N. (B.) sanctaeluciense* remains unresolved.

Our study, based on the original material plus new material, clearly shows that *N. (N.) sanctaeluciense* is quite variable as far as ornament and coiling is concerned, plus the effects of probable dimorphism. A comparable wide range of variation was shown in *Didymoceras awajiense* (Yabe) by Morozumi (1985: 35, pl. 10 (figs 1–4), pl. 11 (fig. 1), pl. 12 (figs 1–2), pl. 13 (figs 1–2), pl. 14 (figs 1–2), pl. 15 (figs 1–3), text-figs 9–11) from the upper Campanian of Awaji Island, Japan. This includes specimens with a nearly planispiral phragmocone (Morozumi 1985, pl. 10 (fig. 4)), to specimens with a high turreted spire (Morozumi 1985 pl. 13 (fig. 2), pl. 14 (fig. 1)). Apart from being older (Campanian), *D. awajiense* has different ornament—on the body chamber virtually every rib is bituberculate—in contrast to the irregular tuberculation in *N. (B.) sanctaeluciense*. On account of the regular coiling of the early whorls, we suggest that *D. awajiense* should also be referred to the subgenus *N. (Bostrychoceras)*.

*Nostoceras (N.) fischeri* (Brunnenschweiler, 1966) (in Henderson *et al.* 1992: 136,

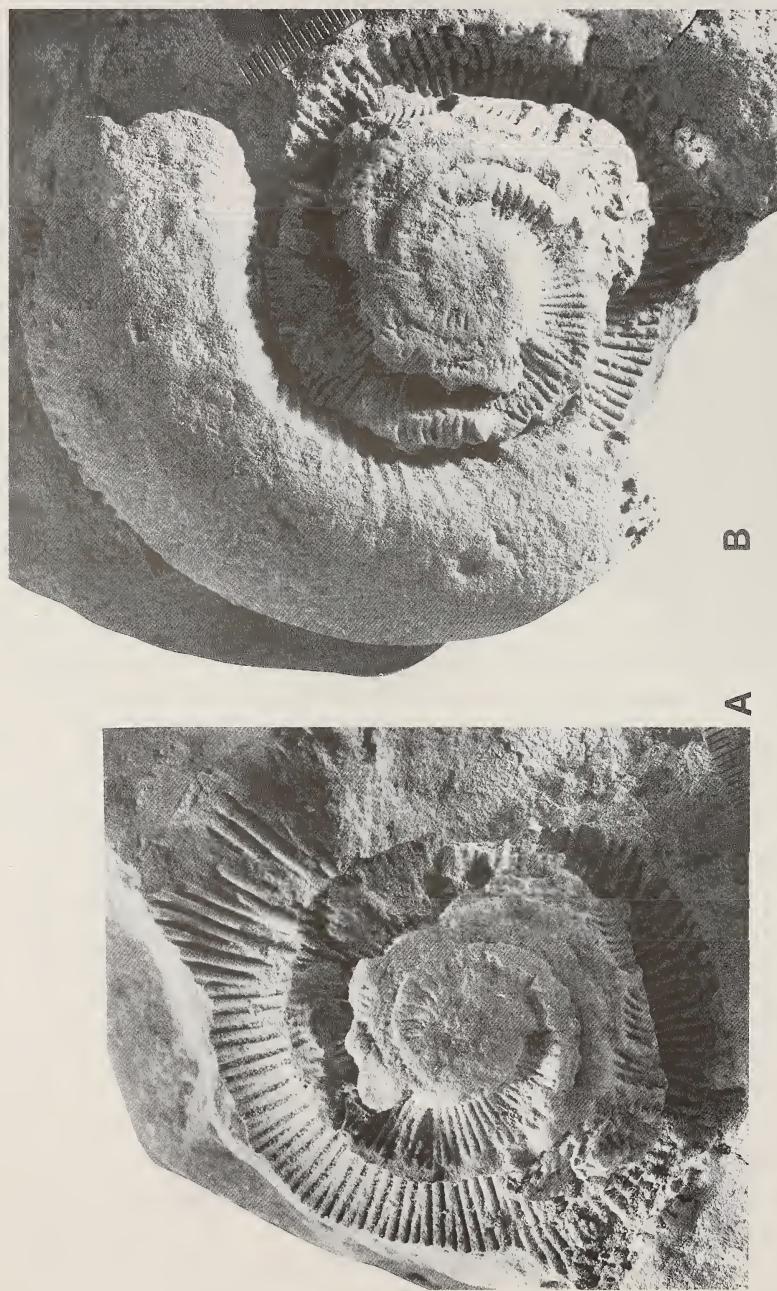


Figure 19

*Nostoceras (Bostrychoceras) sanctaeluciae* (Klinger, 1976). A-B. SAM-PCZ10499. The same specimen with and without the outer whorl. Again, note absence of early, irregular whorls. From locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b. Both  $\times 1$ .

figs 2D–H, 3, 4A–C) from the lower Maastrichtian nodule bed of the Korojon Calcarenite of Western Australia is unfortunately represented by a few specimens only. The ornamentation of the body chamber is very similar to that of *N. (B.) sanctaeluciense*. The size difference between the largest and smallest of the body chamber hooks is comparable to that of the KwaZulu material, and Henderson *et al.* (1992: 138) have also suggested that this may be indicative of dimorphism. None of the Western Australian specimens, however, reaches such large sizes as our KwaZulu material. The largest diameter of the helicoid stage in the former is only 56 mm, compared to 85 in *N. (B.) sanctaeluciense*.

#### *Occurrence*

Lower Maastrichtian, Maastrichtian a and b of KwaZulu and possibly Seymour Island, Antarctica.

#### Genus *Didymoceras* Hyatt, 1894

[=*Emperoceras* Hyatt, 1894; *Didymoceratoides* Kennedy & Cobban 1993b (*fide* Kennedy *et al.* 2000); =?*Cirroceras* Conrad, 1868 *nom. dub.*]

#### *Type species*

*Ancyloceras nebrascense* Meek & Hayden (1857: 71) by original designation of Hyatt (1894: 574).

#### *Diagnosis*

Generally large forms; initial whorls irregular, followed by loosely coiled helical section and large retroversion body chamber. Ornament generally of numerous ribs, and two rows of tubercles which may be irregularly developed.

#### *Occurrence*

*Didymoceras* is best known from North America (see Kennedy *et al.* 2000), but also occurs in Canada, Mexico, The Netherlands, France, Spain, Poland, Israel, Madagascar, KwaZulu, Angola and Nigeria.

#### Subgenus *Didymoceras* (*Didymoceras*) Hyatt, 1894

#### *Type species*

*Ancyloceras nebrascense* Meek & Hayden (1857: 71), by original designation of Hyatt (1894: 574).

#### *Diagnosis*

Early whorls irregular, sometimes hamitid, followed by loosely coiled helix and ending in retroversion body chamber hook. Ornament consists of ribs and two rows of tubercles which may be irregularly developed. Generally large.

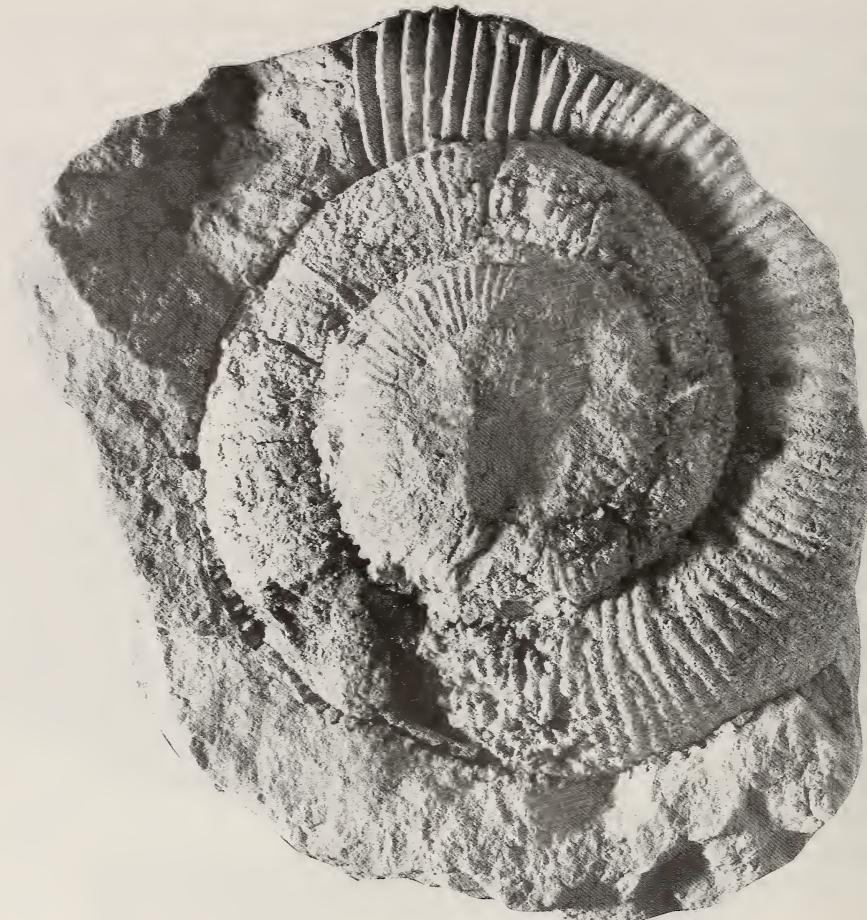


Figure 20

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ10495 from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 1$ .

#### Discussion

*D. (Didymoceras)* differs from *D. (Eodidymoceras)* subgen. nov. (to be described below) in being much larger, and by the distinct retroversal body chamber hook suspended below the phragmocone. It differs from *N. (Nostoceras)* by the irregular early whorls and by its generally much larger size.

#### Occurrence

The subgenus is best known from the Campanian and Maastrichtian of the U.S. Western Interior, but has also been recorded from the Gulf Coast region, California, the Atlantic Seaboard, Colombia, France, northern Spain, Austria, Poland, Russia, Nigeria, Angola, KwaZulu, Madagascar, ?Israel and Japan.



Figure 21

*Nostoceras (Bostrychoceras) sanctachucienense* (Klinger, 1976). A. SAM-PCZ17341 (ex 1167) from locality 120, KwaZulu. B. SAM-PCZ10498 (ex A2016) from locality 113, KwaZulu. Specimen with part of original ribbing preserved and the interspaces filled with sediment. Both from the St Lucia Formation, Maastrichtian a or b. Both.  $\times 1$ .

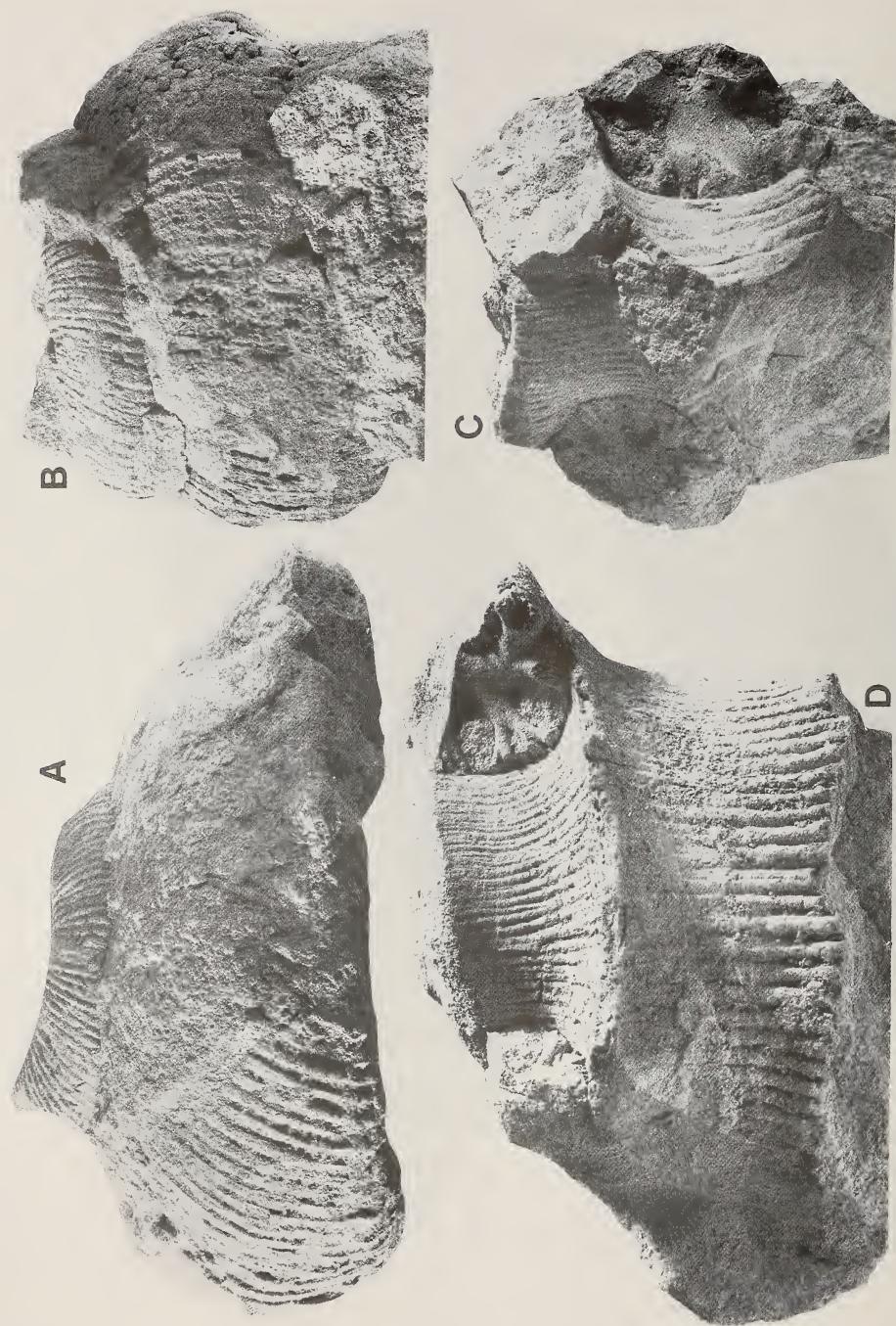


Figure 22



Figure 23

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ10506 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. Specimen with acute apical angle on phragmocone.  $\times 0.83$ .

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Fig. 22. (see facing page). *Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). A. SAM-PCZ10494 from locality 119, KwaZulu. B. SAM-PCZ7927 imprecisely located from 'The Coves', localities 118-121, KwaZulu. C. SAM-PCZ17343 from the same locality. D. SAM-PCZ10493 from locality 125, KwaZulu. All from the St Lucia Formation, Maastrichtian a or b. All specimens with acute apical angle of phragmocone. All  $\times 1$ .



Figure 24

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ10500 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. Part of recurved body chamber with preserved, constricted aperture.  $\times 1$ .

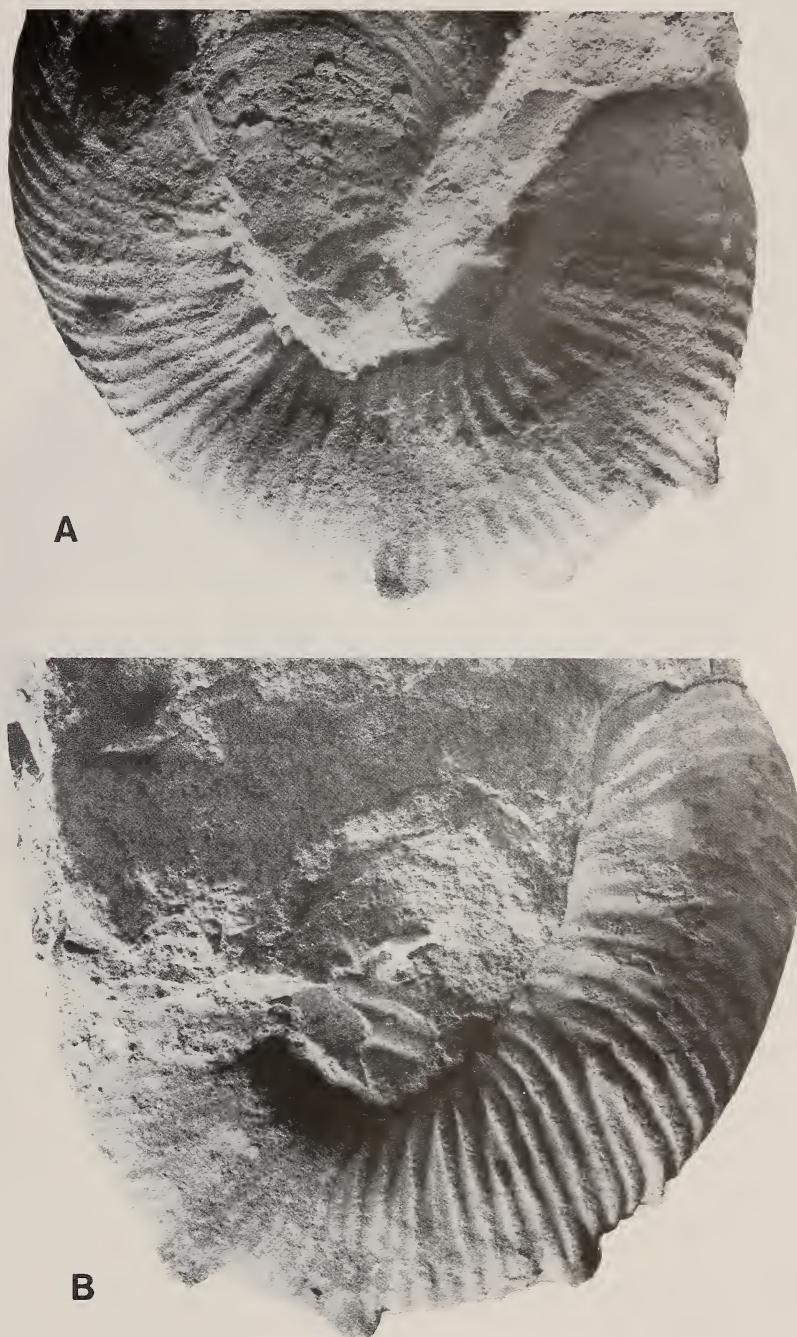


Figure 25

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). A. SAM-PCZ7902 imprecisely located from 'The Coves', localities 118-121, KwaZulu. Specimen with constricted aperture preserved. B. SAM-PCZ17344 from the same locality. Both from the St Lucia Formation, Maastrichtian a or b. Both  $\times 1$ .



Figure 26

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ10501 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. Specimen with recurved body chamber hook.  $\times 1$ .



Figure 27

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ17345, imprecisely located from 'The Coves', localities 118-121, KwaZulu, St Lucia Formation, Maastrichtian a or b. Ventral view of recurved body chamber showing strong, irregular tuberculation.  $\times 1$ .



Figure 28

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAS-Z2251 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Recurved body chamber hook showing transition from single row of tubercles to bituberculate ornamentation.  $\times 1$ .



Figure 29

*Nostoceras (Bostrychoceras) sanctaelucienense* (Klinger, 1976). SAM-PCZ9328 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Part of last helical whorl and recurved body chamber of adult microconch.  $\times 1$ .



Figure 30

*Nostoceras (Bostrychoceras) sanctaeluciae* (Klinger, 1976). SAM-PCZ9328 from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Microconch with recurved body chamber suspended at right angles below base of helical phragmocone.  $\times 1$ .



Figure 31

*Nostoceras (Bostrychoceras) sanctaeluciae* (Klinger, 1976). SAM-PCZ17346 imprecisely located from 'The Coves', localities 118-121, KwaZulu, St Lucia Formation, Maastrichtian a or b. Macroconch with last part of helical section and recurved body chamber hook preserved. Note impression of ventral tubercles on inner edge of last part of helical section.  $\times 0.5$ .



Figure 32

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ9431 (ex 113E) from bed E at locality 113, KwaZulu, St Lucia Formation, Maastrichtian b. Macroconch, part of last helical whorl and recurved body chamber.  $\times 0.58$ .



Figure 33

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ17341 (ex SAS-H116/7 from locality 120, KwaZulu, St Lucia Formation, Maastrichtian b.  $\times 1$ .



Figure 34

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ10504 imprecisely located from 'The Coves', localities 118-121, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 0.7$ .



Figure 35

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ10504 imprecisely located from 'The Coves', localities 118-121, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 1$ .



Figure 36

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ10507 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 1$ .

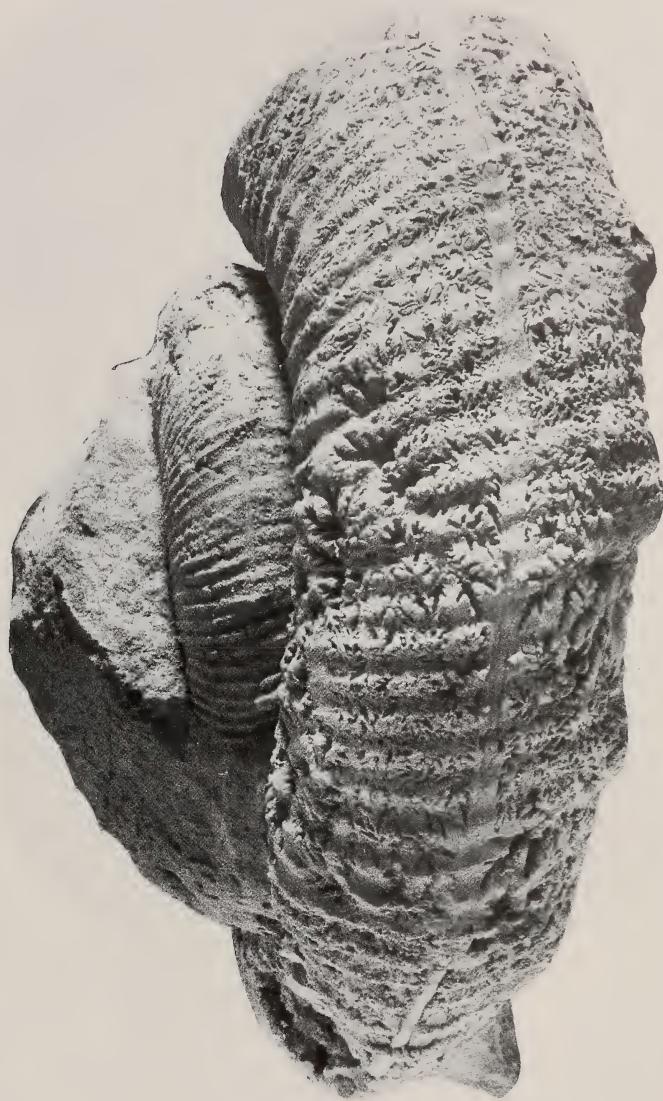


Figure 37

*Nostoceras (Bostrychoceras) sanctaeliciense* (Klinger, 1976). SAM-PCZ10507 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 1$ .



Figure 38

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ10507 from locality 125, KwaZulu, St Lucia Formation, Maastrichtian a or b. View of venter of last phragmocone whorl and impression of recurved body chamber.  $\times 1$ .



Figure 39

*Nostoceras (Bostrychoceras) sanctaeliciense* (Klinger, 1976). A. SAM-PCZ17349 (ex SAS-H115/15). B. SAM-PCZ17350 (ex SAS-H115/13). Both from locality 120, KwaZulu, St Lucia Formation, Maastrichtian a or b. Ventral view of specimens to show appearance of abapical tubercles. Both  $\times 1$ .

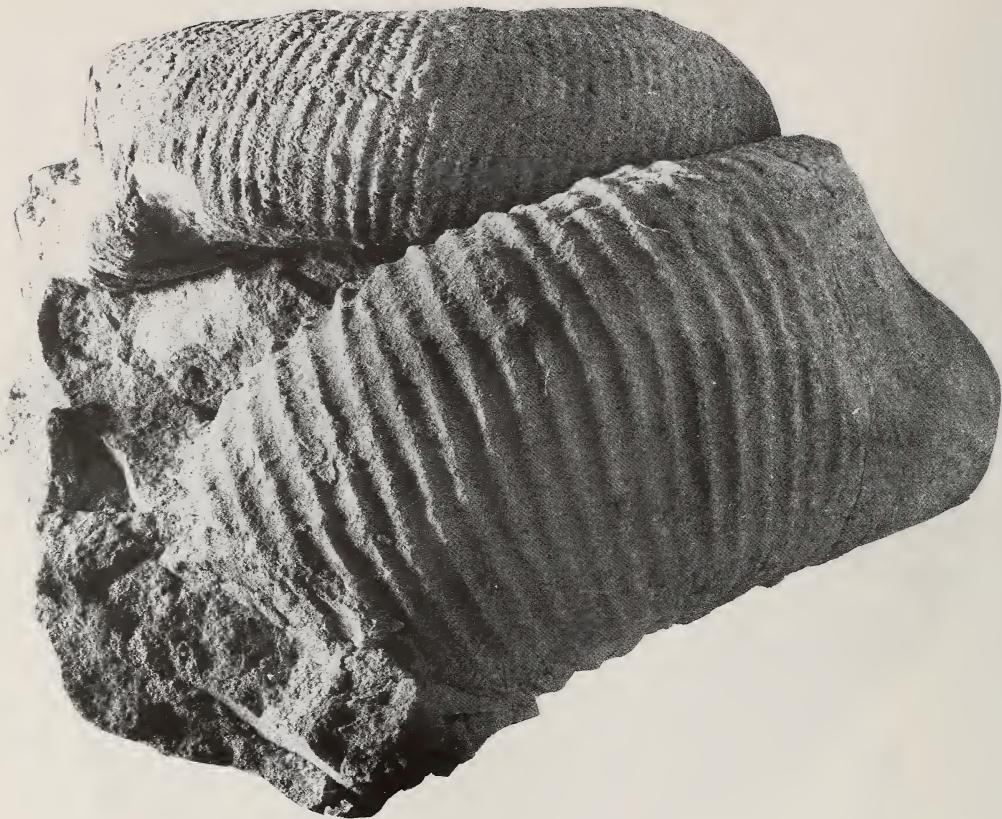


Figure 40

*Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ10504 imprecisely located from 'The Coves', localities 118-121, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 1$ .

***Didymoceras (D.) australis* sp. nov.**

Figs 41-44, 50B-C

*Type*

Holotype is SAM-PCZ17351 from locality 109C, western part of Nibela Peninsula, KwaZulu, St Lucia Formation, Campanian III.

*Material*

SAM-PCZ7576 and SAM-PCZ9332, both from the same locality as the holotype. SAM-PCZ18749, SAM-PCZ18748, NMB-D1490, all presumably from the same locality.

*Etymology*

Named for its occurrence in the southern hemisphere.



Figure 41

*Didymoceras (Didymoceras) australis* sp. nov. The holotype, SAM-PCZ17351 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. With part of what appears to be an anaptychus (arrow).  $\times 0.8$



Figure 42

*Didymoceras (Didymoceras) australis* sp. nov. The holotype, SAM-PCZ17351 from locality 109c, KwaZulu, St Lucia Formation, Campanian III.  $\times 0.8$ .



Figure 43

*Didymoceras (Didymoceras) australis* sp. nov. The holotype, SAM-PCZ17351 from locality 109c, KwaZulu, St Lucia Formation, Campanian III.  $\times 0.8$ .

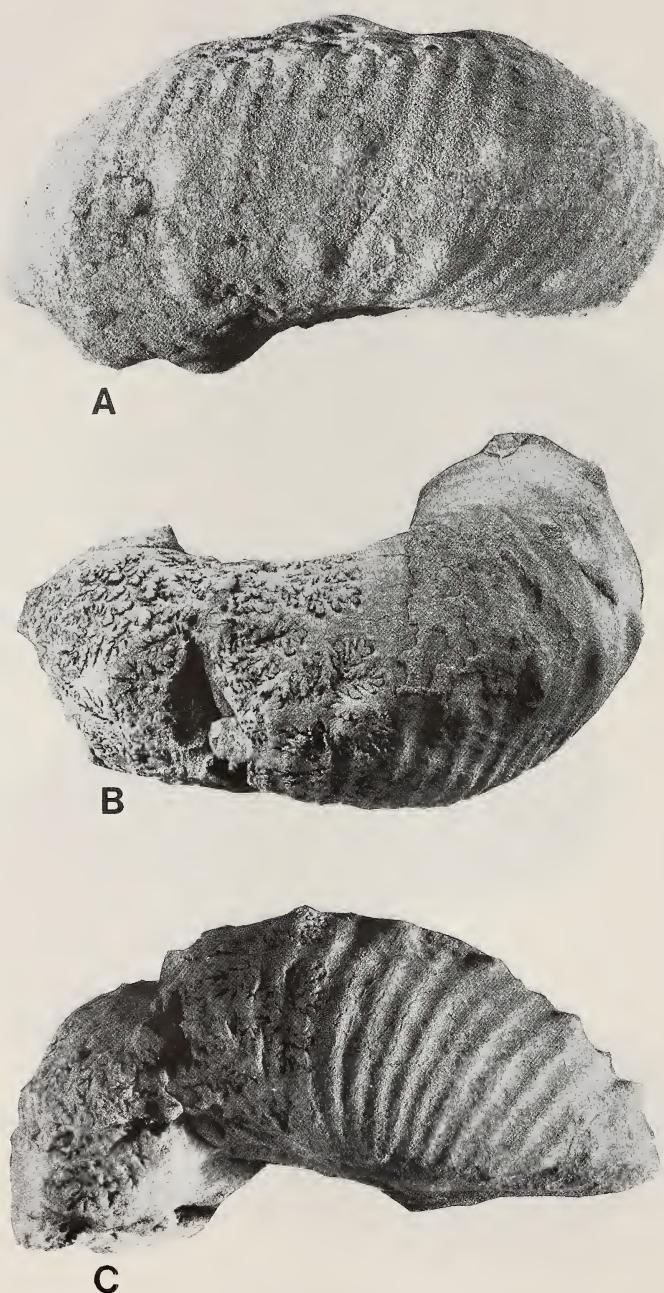


Figure 44

*Didymoceras (Didymoceras) australis* sp. nov. SAM-PCZ7576 from locality 109c, KwaZulu, St Lucia Formation, Campanian III.  $\times 1$ .

### Description

The holotype SAM-PCZ17351 consists of at least two helically coiled whorls of which the last half a whorl is non-septate. The paratypes all consist of less than half a whorl.

Ornament on the phragmocone consists of low, dense ribbing and two large, but weakly developed and irregularly spaced rows of tubercles—one just below the siphuncle and the other near the abapical part of the whorl. Ornament becomes stronger on the body chamber and sharp-crested ribs are conspicuous, but the tubercles are still poorly developed.

The suture line is extremely complex. A structure resembling an anaptychus is situated between the early whorls of the holotype (Fig. 41, arrow). We do not know if this structure belongs to the present species or to the associated ammonite fauna.

### Discussion

Size, coiling and ornament clearly distinguish this specimen from all other known KwaZulu nostoceratids.

The closest match we can find with our material is *D. (D.) nebrascense* from the upper Campanian of the U.S. Western Interior. The reconstruction in Scott & Cobban (1965) (see also Gill & Cobban 1973, fig. 5a; Kennedy *et al.* 2000: 7, figs 3–4, 6–7, 8c, d, 9–13, 62) shows loose, helical coils and poorly developed tuberculation on the phragmocone, compared to the stronger ornament in the younger *D. (D.) stephensoni* and *D. (D.) cheyennense*.

### Occurrence

Campanian III of KwaZulu.

*Didymoceras (Didymoceras) sp.*

Fig. 45

### Material

SAM-PCZ7638 from locality 109C, the western part of Nibela Peninsula, KwaZulu, St Lucia Formation, Campanian III.

### Description and discussion

A single specimen differs from *Didymoceras (D.) australis* in being much larger and still septate at a diameter of c. 50 mm, and in having tighter coiling. This specimen may connect with the largest fragment of *D. (D.) australis*, SAM-PCZ7576 in having a similar mode of ornamentation. It is possible that the differences in size are due to dimorphism, but with the limited material available, it is impossible to say with certainty.

### Occurrence

Campanian III of KwaZulu.



Figure 45

*Didymoceras (Didymoceras) sp.* SAM-PCZ7638 from locality 109c, KwaZulu, St Lucia Formation, Campanian III.  $\times 1$ .

***Didymoceras (Didymoceras?) africanum* sp. nov.**  
Figs 46, 47A–C

*Type*

Holotype by monotypy is SAM-PCZ7637 from locality 109C, western part of Nibela Peninsula, KwaZulu, St Lucia Formation, Campanian III.

*Etymology*

Named after its geographic occurrence.

*Description*

The holotype consists of a large, virtually planispirally coiled half of a whorl, part of an earlier whorl impressed in the matrix of the former on the inner adapical edge, and a fragment of an even earlier whorl, found loose in the same block of matrix.

Coiling in the spiral section of the shell is extremely loose, forming a low spire with a very wide umbilicus. Ornament consists of numerous, sharp-crested ribs. These are weak on the inner (dorsal) side of the whorl, and strongest on the adapical and abapical parts of the whorls. Two rows of tubercles are situated on the ventral (siphonal) part of the whorls. The first is slightly adapical of the midline and the second just above the abapical edge. These are connected adapically and abapically by irregularly looped or single ribs; some of the ribs are not connected to tubercles at all. In the area between the tubercles the ribs weaken and form loops or are connected in a zig-zag pattern (Fig. 47B–C).

*Discussion*

The asymmetric position of the tubercles on the venter (flanks) and the impression of a smaller whorl above the largest suggest that this is indeed a very low-spired species of *Didymoceras*, and not, perhaps, a representative of *Exiteloceras*, *Lewyites*, or *Neancyloceras*. *Exiteloceras jenneyi camacki* Kennedy *et al.* (2000: 62, figs 44D, 49–50) is superficially similar to the present species as far as the large size is concerned, but differs in being planispirally coiled.

The low coiling and consistent, strongly bituberculate ornament easily distinguishes *D. (D.?) africanum* from the coeval *D. (D.) australis*, as well as from the younger *N. (Bostrychoceras) sanctaeluciense*. Some specimens of *N. (B.) awajiense* (Yabe) figured by Morozumi (e.g. 1985, pl. 10 (fig. 4a–c)) have a similar very low apical angle, but again the coarser ribbing and regular bituberculation distinguish *D. (D.?) africanum* from this Japanese species.

*Occurrence*

Campanian III of KwaZulu.



Figure 46

*Didymoceras (Didymoceras?) africanum* sp. nov. The holotype, SAM-PCZ7637, from locality 109c, KwaZulu, St Lucia Formation, Campanian III.  $\times 1$ .

Subgenus *Didymoceras* (*Eodidymoceras*) subgen. nov.*Type species*

*Nostoceras hyatti* Stephenson var. *mitraikyensis* Collignon (1970: 67, pl. 614 (fig. 2293)) from the middle Campanian of Madagascar and lower Campanian of KwaZulu.

*Etymology*

*Eos*, indicating the dawn or origin of the genus *Didymoceras*.

*Diagnosis*

Major part of shell coiled in a loose helix or possibly even criocone, body chamber curves upwards. Ornament consists of bituberculate and non-tuberculate ribs. Some ribs are both flared and bituberculate. Constrictions may be present. Early whorls possibly irregular.

*Discussion*

This subgenus is erected for the earliest representatives of *Didymoceras* s.l. They differ from *Didymoceras* s.s. mainly in being smaller and in having more regular, corkscrew-like coiling on the major part of the phragmocone, and the upwards-facing aperture as in the majority of *Eubostrychoceras* (*E.*) species. The regular ornamentation consisting of tubercles on all, or on alternate ribs, some with constrictions and flared bituberculate ribs also separates *D. (Eodidymoceras)* from *Didymoceras* s.s. This lineage appears to continue in the middle Campanian of the U.S. Western Interior as *Didymoceras cochleatum* (Meek & Hayden, 1859) and in the upper Campanian as *Didymoceras binodosum* Kennedy & Cobban, 1993). The genus *Cirroceras* Conrad, 1868 (type species *Ammonoceratites conradi* Morton, 1841: 109; 1842: 212, pl. 10 (fig. 1)) is generally regarded as a synonym of *Didymoceras*. The genus was revived, however, by Kennedy *et al.* (2000: 11) for forms coiled in a loose helix and with an upward curving aperture. Thus as far as coiling is concerned, *Cirroceras* is very close if not indistinguishable from *D. (Eodidymoceras)*. The main differences are that in *Cirroceras*, of the two rows of tubercles, those of the lower row are larger, and constrictions are absent. In addition, *Cirroceras* is only known with certainty from the upper part of the upper Campanian. If *Cirroceras* is to be considered a valid taxon, it should possibly be regarded as a subgenus of *Didymoceras*. It is possibly derived from the *D. (Eodidymoceras)* lineage.

Unfortunately our material is limited, but all three KwaZulu and Madagascan species to be described below show distinct *Allocrioceras*-like features, thus suggesting that the origins of the *Nostoceratidae* may be sought in that genus.

*Occurrence*

Lower Campanian of KwaZulu; middle Campanian of Madagascar; ?middle and upper Campanian of the U.S. Western Interior.

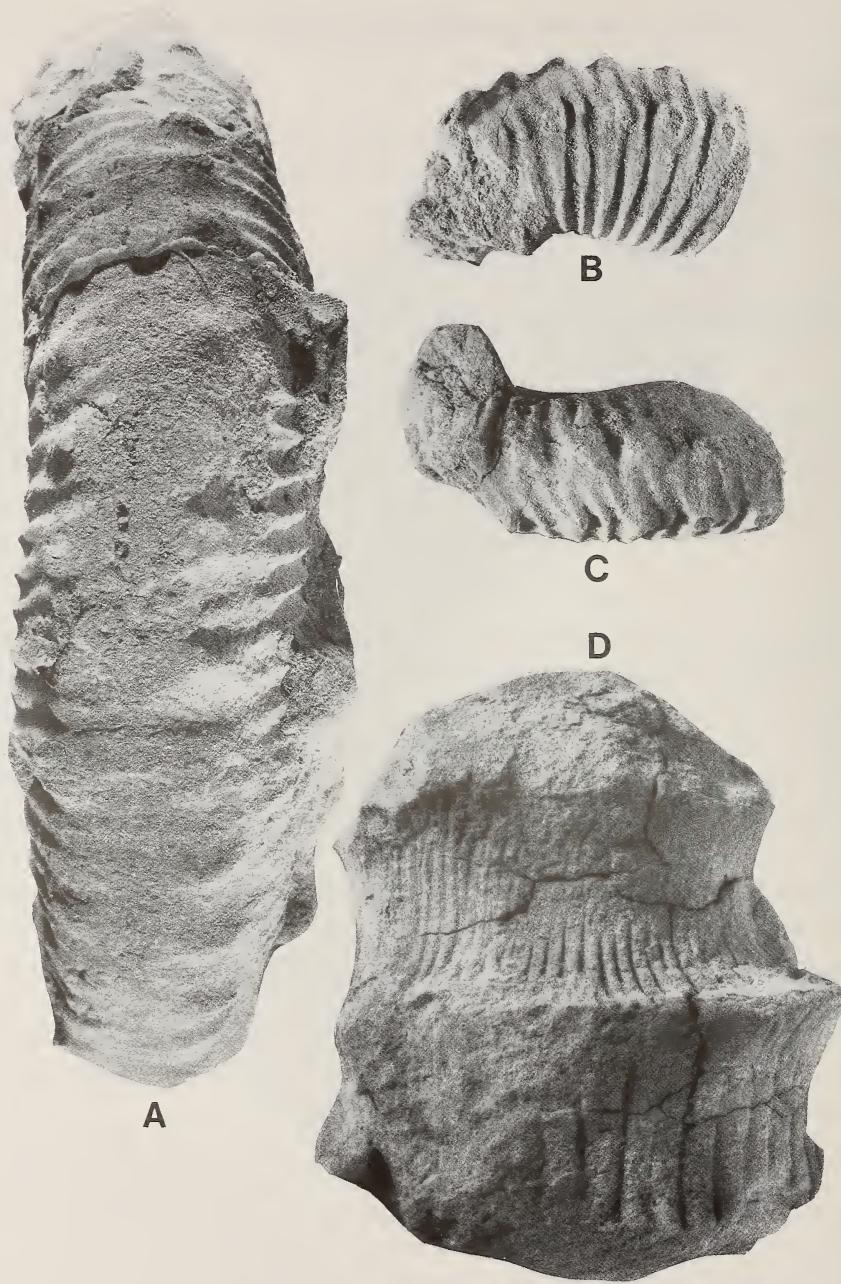


Figure 47

A-C. *Didymoceras (Didymoceras?) africanum* sp. nov. The holotype, SAM-PCZ7637 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. A. The outer whorl. B-C. Fragment of inner whorls impressed into the outer whorl. Note the asymmetry of the ornamentation, indicative of low, helical rather than planispiral coiling. D. *Nostoceras (Bostrychoceras) sanctaeluciense* (Klinger, 1976). SAM-PCZ17352, probably from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Impression of phragmocone of specimen with acute apical angle. All  $\times 1$ .



Figure 48

*Didymoceras (Eodidymoceras) mitraikyense* (Collignon, 1970). A–B. SAM-PCZ18754 (ex WJK 4/D) from locality 14, KwaZulu, St Lucia Formation, lower Campanian. C–D. The holotype, GD11293 from Gisement 148, Mitraiky (Antsalova), Madagascar, middle Campanian, Zone of *Pachydiscus grossouvrei*. Note upward curvature of body chamber.  $\times 1$ .

*Didymoceras (Eodidymoceras) mitraikyense* (Collignon, 1970)  
Fig. 48

?1969 *Nostoceras* sp. Collignon, p. 46, pl. 530 (fig. 2092).  
 1970 *Nostoceras hyatti* Stephenson var. *mitraikyensis* Collignon, p. 67, pl. 614 (fig. 2293).  
 1976 *Didymoceras (Didymoceras) schloenbachi schloenbachi* (Favre, 1869); Klinger, p. 67, pl. 29 (fig. 4), pl. 30 (fig. 4).

*Type*

Holotype is the specimen figured by Collignon (1970, pl. 614 (fig. 2092)) GD11293 (Fig. 48C–D) from the middle Campanian, of Gisement 148, Mitraiky (Antsalova), Madagascar.

*Material*

SAM-PCZ18754 from locality 14, KwaZulu, St Lucia Formation, lower Campanian.

*Description*

No new material has been found since Klinger's (1976) original description, but several pieces have been fitted together to form a helix consisting of about three and a half whorls. Coiling is sinistral, forming a regular, loose corkscrew, with the whorls separated by intervals of approximately one whorl height. The holotype (Fig. 48C–D) shows that the last part of the body chamber curves upwards in *Eubostrychoceras* (*E.*)-fashion.

Ornament consists of about 30 single, radial to slightly rursiradiate ribs per whorl. Each alternate rib bears two rows of tubercles, one just below midflank, and the other at the abapical edge.

*Discussion*

Following Wiedmann's (1962: 204) interpretation of *Helicoceras schloenbachi* Favre (1869: 30, pl. 7 (fig. 5)), Klinger (1976: 67) referred the KwaZulu material to that species. However, Blaszkiewicz (1980) and Kennedy & Summesberger (1987: 31) suggested that all Campanian specimens referred to *schloenbachi* belong elsewhere. In the case of loosely coiled specimens such as the KwaZulu material, Kennedy & Summesberger (1987: 31) suggested that they may even belong to different genera.

As far as the loose, helical coiling, and ornament on the phragmocone are concerned, *D. (Eodidymoceras) mitraikyense* is very similar to *D. (D.) pueblocense* Cobban *et al.* (1997: 225, figs 2–5) from the upper Campanian of Colorado and Wyoming. That species, however, has the typical U-shaped body chamber suspended below the phragmocone, and large size of *Didymoceras* s.s.

Fragments of *D. (E.) mitraikyense* are virtually indistinguishable from helically coiled species of *Allocrioceras*, e.g. *A. billinghami* Klinger, 1976 (see Fig. 52E–F). Again, we are not quite sure of the exact relationships between the two genera but, as suggested above, it seems to confirm our view that at least some of the Nostoceratidae can trace their origins to *Allocrioceras* during the Turonian.

A few species of *Didymoceras* show loose coiling similar to that of *D. (E.) mitraikyense*, but in all the cases the ornament is sufficiently different to distinguish between these. *D. (D.) donezianum* (Mikhailov, 1951), recently reviewed by Kennedy & Cobban (1993c: 137) has loose coiling in the early stages, but the body chamber becomes closely coiled. *Didymoceras (D.) navarroense* (Shumard, 1861) (see Stephenson 1941: 417, pl. 83 (figs 9–13)), and Kennedy & Cobban (1993a: 421, figs 12.1, 13.1–13.8, 14.1–14.4, 14.13, 14.14) has more robust ornament, and numerous fine looped and intercalatory ribs. *Didymoceras (D.) subtuberculatum* Howarth (1965: 374, pl. 7 (figs 2–6), pl. 11 (fig. 4)) has similar loose coiling on the phragmocone, and regularly-spaced, flared ribs; it may possibly be referred to *D. (Eodidymoceras)*.

#### *Occurrence*

Lower Campanian of KwaZulu, lower? and middle Campanian of Madagascar.

#### *Didymoceras (E.) howarthi* sp. nov.

Figs 49, 50A, 51

#### *Type*

Holotype, by monotypy is SAM-PCZ7349 from locality 74, Die Rooiwalle, KwaZulu, St Lucia Formation, probably from the lower Campanian, but possibly uppermost Santonian.

#### *Etymology*

Named for Dr M. K. Howarth of the Natural History Museum, London.

#### *Description*

The holotype consists of two and a half whorls of a loosely coiled helix. Ornament consists of 34 minor and major ribs per whorl. These are narrow and high-crested, separated by much wider interspaces. The minor ribs bear two rows of minute tubercles, the first slightly above the midline and the other near the abapical quarter of the flanks. About 5 major flared ribs occur per whorl. These are flanked adaperturally by a wide constriction. Where sufficiently well preserved, these can also be seen to bear two rows of tiny pointed tubercles.

#### *Discussion*

With respect to the loose coiling of the phragmocone, bituberculate normal and flared ribs and constrictions, *D. (E.) howarthi* is very similar to *D. cochleatum* (Meek & Hayden 1859) (see Kennedy *et al.* 1999) from the middle Campanian of South Dakota and Wyoming and *D. binodosum* (Kennedy & Cobban 1993b) from the upper Campanian of the U.S. Western Interior and Gulf Coast. Neither of these two species, however, has as loose coiling as *D. (E.) howarthi*. It is possible that *D. (E.) howarthi* gave rise to this middle to upper Campanian lineage.

Another comparable species is *Didymoceras subtuberculatum* Howarth (1965: 374,



Figure 49

*Didymoceras (Eodidymoceras) howarthi* sp. nov. The holotype, SAM-PCZ7349 from locality 74, Die Rooiwalie, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. Note the strong constriction with associated flared rib and weak bituberculate ornament on all ribs.  $\times 1$ .



Figure 50

A. *Didymoceras (Eodidymoceras) howarthi* sp. nov. The holotype, SAM-PCZ7349 from locality 74, Die Roodwalle, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. B-C. *Didymoceras (Didymoceras) australis* sp. nov. NMB-D1490 from locality 109c, KwaZulu, St Lucia Formation, Campanian III. Both  $\times 1$ .

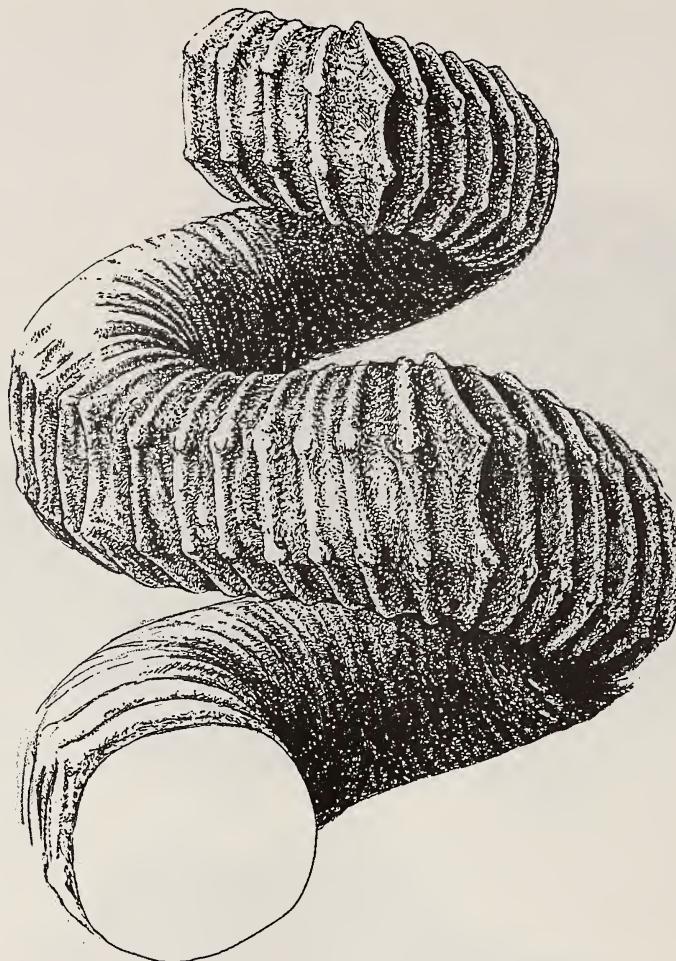


Figure 51

*Didymoceras (Eodidymoceras) howarthi* sp. nov. Reconstruction of the holotype, SAM-PCZ7349, by Samantha Black.  $\times 1$ .

pl. 7 (figs 2–6), pl. 11 (fig. 4)) from the uppermost Campanian or basal Maastrichtian of Angola. This species could possibly also be referred to the subgenus *D. (Eodidymoceras)* as mentioned above. In *D. (D.) subtuberculatum*, however, the minor ribs are more numerous and finer, and the flared ribs far more prominent than in *D. (E.) howarthi*. Also, the two rows of tubercles in *D. (D.) subtuberculatum* are much more prominent, and placed near the base of the whorls, rather than on the flanks. The specimen from the lower Campanian of Madagascar described by Collignon (1969: 42, pl. 529 (fig. 2086)) as *Didymoceras subtuberculatum* may possibly also be referred to this species.

#### *Occurrence*

Possibly uppermost Santonian but probably lower Campanian of KwaZulu.



Figure 52

A-D. *Didymoceras (Eodidymoceras?)* sp. SAM-PCZ18751 (ex Z2071) from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. Note the bituberculate flared rib, reminiscent of *Allocrioceras* ornamentation. E-F. *Allocrioceras billinghami* Klinger, 1976. SAM-PCZ18752 (ex Z1598) from locality 92, KwaZulu, St Lucia Formation, Coniacian II or III. Note the close resemblance to *Didymoceras (Eodidymoceras) mitraikyense* (Collignon, 1969). Both  $\times 1$ .

*Didymoceras (Eodidymoceras?)* sp.

Fig. 8E, 52 A–D

1976 *Hyphantoceras (Madagascarites?) amapondense* (Van Hoepen); Klinger p. 71 pars, pl. 33 (fig. 2) only.

1994 *Allocrioceras* Cooper, p. 365, fig. 1f–g.

1997 *Eubostrychoceras (Amapondella) amapondense* (Van Hoepen); Klinger & Kennedy 1997, p. 245, fig. 15E only.

1997 'Allocrioceras' sp. Klinger & Kennedy, p. 246, fig. 16.

*Material*

SAM-PCZ18751 (ex Z2071a–b), SAM-PCZ12949 from locality 105, St Lucia Formation, KwaZulu, uppermost Santonian or basal Campanian.

*Description*

Unfortunately this species is based on fragments only. The most complete, SAM-PCZ18751 (Fig. 52A–D), consists of less than a third of an apparently crioceratitid whorl. The whorl section is circular; ornament consists of major, bituberculate ribs separated by three to four subsidiary, non-tuberculate ribs. The tubercles of the major ribs are extremely delicate. SAM-PCZ12949 (Fig. 8E) is a latex peel consisting of a large specimen with bituberculate major ribs and non-tuberculate intermediary ribs. Part of a *Glyptoxoceras*-like whorl occurs with this specimen. We do not know if the two specimens belong to the same individual; if they do, it suggests that the early whorls of *Didymoceras (Eodidymoceras)* may be irregular, as in later *Didymoceras* s.s. spp.

*Discussion*

If these specimens were found in isolation and without a Santonian/Campanian date, we would not hesitate to refer them to *Allocrioceras*, as was done by Cooper (1994, fig. 1F–G). This genus, however, is generally limited to the Cenomanian to Coniacian Stages. However, the similarities between *Allocrioceras* and *D. (Eodidymoceras)* are so striking, that we doubt if these similarities are purely homoeomorphic, as previously mentioned.

*Occurrence*

Upper Santonian and/or lower Campanian of Pondoland, KwaZulu and Madagascar (HCK pers. obs.)

**Family Diplomoceratidae Spath, 1926**

(= Family Solenoceratidae Cooper, 1994; Family Neocrioceratidae Spath, 1953)

Subfamily Diplomoceratinae Spath, 1926

(= Scalaritinae Ward, 1976)

Genus *Diplomoceras* Hyatt, 1900

[= *Eudiplomoceras* Brunschweiler, 1966]

*Type species*

*Baculites cylindracea* Defrance, 1816 by original designation of Hyatt (1900: 160).

*Diagnosis*

Shell consists of three or more parallel shafts, closely spaced, but not in contact. Whorl section varies from compressed through circular to depressed. Ornament consists of fine, sharp-crested, dense ribbing. Internal moulds are generally, but not always smooth. Suture deeply incised and complex. The shell may reach very large size, with body chambers over a metre in length.

*Discussion*

Klinger (1976) followed Wiedmann (1962) in regarding *Glyptoxoceras* as a subgenus of *Diplomoceras*. The recent descriptions of well-preserved and abundant specimens of *Glyptoxoceras* from south India (Kennedy & Henderson 1992), Western Australia (Henderson *et al.* 1992), France (Kennedy 1992a), British Columbia (Ward & Mallory 1977) and California (Matsumoto 1959) all show that the coiling strategies in *Glyptoxoceras*, albeit very variable, differ sufficiently from those of *Diplomoceras* to warrant separate generic status.

Following the extensive revision of the type species, *D. cylindraceum* by Kennedy (1987) it appears that the genus is monospecific. All the other 'species' referred to *Diplomoceras* are either synonyms of *D. cylindraceum* or based on uninterpretable material.

The systematics, affinities, stratigraphic and geographic distribution and possible origins of the type species, *Diplomoceras cylindraceum* are discussed fully by Klinger & Kennedy (This volume 110 (4)).

*Occurrence*

Where precisely dated, *D. cylindraceum* typically occurs in the Maastrichtian, but there are reports of the species from the upper Campanian of Tercis, France (Küchler & Odin 2001) and Piotrawin, Poland (Machalski 1996). Other specimens, described mainly as *D. lambi* or *D. notabile* are also recorded from the Campanian, even ranging down as far as the lower Campanian (e.g. Alabushev & Wiedmann 1997).



Figure 53

*Diplomoceras cylindraceum* (Defrance, 1816). SAM-PCZ17355 (ex SAS-A432) from locality 111, KwaZulu, St Lucia Formation, Campanian III.  $\times 1$ .

*Diplomoceras cylindraceum* (Defrance, 1816)  
Figs 53–55

1816 *Baculites cylindracea* Defrance, p. 160.

1976 *Diplomoceras (Diplomoceras) notabile* Whiteaves; Klinger, p. 82, pl. 33 (figs 2a–b, 4a–b).

1987 *Diplomoceras cylindraceum* (Defrance); Kennedy, p. 181, pl. 17 (fig. 3), pl. 18 (fig. 5), pl. 21 (figs 2–3, 5–6), pl. 22 (fig. 6), pl. 23 (figs 1–2), pl. 24 (figs 1–3), pl. 25 (figs 1–8), pl. 26 (fig. 18), pl. 33 (fig. 16), pl. 36 (fig. 6), text-figs 9–10 (with full synonymy).

1992 *Diplomoceras cylindraceum* (Defrance); Henderson *et al.*, p. 140, figs 5, 6A–E, H–K, 7.

1992 *Diplomoceras cylindraceum* (Defrance); Kennedy & Henderson, p. 704, pl. 6 (figs 1–3), text-figs 1B, 3.

1993 *Diplomoceras cylindraceum* (Defrance); Hancock & Kennedy, p. 164, pl. 15 (fig. 15), pl. 17 (figs 1–4).

1993 *Diplomoceras cylindraceum* (Defrance); Ward & Kennedy, p. 49, figs 42, 43.16, 43.17.

1997 *Diplomoceras notabile* Whiteaves; Alabushev & Wiedmann, p. 14 pl. 4 (fig. 1).

1999 *Diplomoceras cylindraceum* (Defrance); Kennedy, p. 653, figs 12.1–12.5.

2003 *Diplomoceras cylindraceum* (Defrance); Klinger & Kennedy, figs 1–9.

*Type*

Neotype designated by Kennedy (1987: 183, pl. 24 (figs 1–3)) is no. 10511 in the collections of the Institut Royal des Sciences Naturelles de Belgique from the upper Maastrichtian Nekum or Meerssen Chalk of St Pietersberg near Maastricht in The Netherlands.

*Material*

SAM-PCZ7843, PCZ7943 from bed 7 at locality 20, Maastrichtian II; SAM-PCZ17355 (ex SAS-A432) from locality 111, Campanian III; SAM-PCZ9551 from locality 113, Maastrichtian a or b; SAS-A2080, SAM-PCZ12950 (ex H108/9), PCZ12951 from locality 116, Maastrichtian a, SAM-PCZ7940 from locality 20, Maastrichtian a or b; SAM-PCZ7998 from locality 124, Maastrichtian a or b; SAM-PCZ17356 (ex H105/9) from locality 116, Maastrichtian a or b; SAM-PCZ18707, SAM-PCZ7904, unlocalized from 'The Coves', Maastrichtian a or b. All from KwaZulu and all from the St Lucia Formation.

*Dimensions*

Specimen	MxWb	MxWh	Wb:Wh	MnWb	MnWh	Wb:Wh	Ri
PCZ12950	28	31	0.9				
PCZ7843	40	36	1.1				
PCZ9551	58	64	0.9	39	44	0.9	19
PCZ12951	57	64	0.9	45	56	0.8	16



Figure 54

*Diplomoceras cylindraceum* (Defrance, 1816). SAM-PCZ9551 from locality 113, KwaZulu, St Lucia Formation, Maastrichtian a or b.  $\times 1$ .



Figure 55

*Diplomoceras cylindraceum* (Defrance, 1816). A. SAM-PCZ7940 from locality 20, KwaZulu, St Lucia Formation, Maastrichtian a or b. B. SAM-PCZ7904, an internal mould of the phragmocone showing the typical absence of ornament. C-E. SAM-PCZ17356 (ex H105/9) from locality 116, KwaZulu, St Lucia Formation, Maastrichtian a. All  $\times 1$ .

### Description

All except one of our specimens are parts of the straight shafts of the phragmocone, preserved as internal moulds. The whorl section varies from depressed to near-circular to compressed. All but one of our figured specimens is ornamented by fine, c. 16–19 ribs per whorl height. Their orientation varies from radial to distinctly rursiradiate on the larger specimens. This is rather unusual, as internal moulds of the phragmocone of this species are usually smooth, due to thickening of the nacreous layer beneath the ribs. The sutures are complex and dendritic.

### Discussion

Variation in this species was described in detail by Kennedy (1987) on the basis of more than 70 specimens from the type locality and our material adds nothing new. As mentioned above, various aspects of the species are discussed extensively by Klinger & Kennedy (This volume 110 (4)).

### Occurrence

Where well dated, *D. cylindraceum* is a typical Maastrichtian species, but it has been recorded from as early as Early Campanian. The species has a virtually cosmopolitan distribution; details are provided by Klinger & Kennedy (This volume 110 (4)).

Genus *Glyptoxoceras* Spath, 1925  
(= *Neohamites* Brunnenschweiler, 1966)

### Type species

*Hamites rugatus* Forbes (1846: 116, pl. 11 (fig. 6)), by original designation of Spath (1925: 30).

### Diagnosis

Early whorls variable, straight, criocone, open helix or turriliticone, followed by loose, planispiral elliptical or polygonal whorls. Ornament consists of simple ribs only. Aperture collared and preceded by a constriction.

### Discussion

Due to the open coiling and inherent fragile nature of the shell, complete specimens of *Glyptoxoceras* are a rarity. There is great variation in density of ribbing; this, combined with the incomplete nature of the material means that the systematics of the genus are rather chaotic. At present, only the upper Maastrichtian material from south India, revised by Kennedy & Henderson (1992), and of Western Australia revised by Henderson *et al.* (1992) and *Glyptoxoceras aquisgranense* (Schlüter) from the lower Campanian, based on exquisitely preserved material from Nalzen, France (Kennedy 1992a) are sufficiently defined. Older, Coniacian and Santonian material from Madagascar, KwaZulu and Austria, as well as lower Campanian material from Madagascar, are difficult to separate satisfactorily.

### Occurrence

Coniacian to Maastrichtian, with records from Western Europe, Poland, Russia, Madagascar, KwaZulu, India, Western Australia, British Columbia, California, New Zealand, Brazil, Chile, Jamaica and Japan.

*Glyptoxoceras rugatum* (Forbes, 1846)

Fig. 56C

1846 *Hamites rugatus* Forbes, p. 117, pl. 11 (fig. 2).

1992 *Glyptoxoceras rugatum* (Forbes); Kennedy & Henderson, p. 695, pl. 1 (figs 1–2, 5–16), pl. 2 (figs 10–11, 14–29), pl. 3 (figs 1–3), pl. 4 (figs 2, 12–15), text-fig. 1A, E. (*cum synon.*).

1992 *Glyptoxoceras rugatum* (Forbes); Henderson *et al.*, p. 145, (figs 8–13) (*cum synon.*).

### Material

SAM-PCZ17358 from the locality exposing the contact between the base of the Uloa Formation and the top of the St Lucia Formation at Monzi (see e.g. Cooper & McCarthy 1998: 5, fig. 7a for details). Maastrichtian I or II.

### Description and discussion

A single, straight fragment with a circular section and about five ribs per whorl height is the only specimen referable to this species.

This species is best known from the upper Maastrichtian of Western Australia (Henderson *et al.* 1992) and south India (Kennedy & Henderson 1992). These authors provide an extensive synonymy of the species and show that the various specific names applied, e.g. *subcompressus*, *nereis*, *circulare*, *nipponicum*, *bullarensis*, *giraliensis*, *cardabiensis*, *largesulcatus* and *soufoulisi* all fall within the variation of *G. rugatum*.

### Occurrence

Maastrichtian of south India, KwaZulu, Brazil, possibly Chile, Western Australia, northern Spain, south-east France, The Netherlands and Belgium.

*Glyptoxoceras octocostatum* (Collignon, 1969)

Fig. 56A–B, D–F

1906 *Heteroceras* sp. Woods, p. 339, pl. 42 (fig. 5).

1921a *Diplomoceras?* *indicum* Spath, p. 256, pl. 23 (fig. 5).

1969 *Diplomoceras indicum* Forbes *octocostatum* Collignon, p. 45, pl. 530 (fig. 2090).

1976 *Diplomoceras* (*Glyptoxoceras*) *indicum* (Forbes); Klinger, p. 79, pl. 34 (figs 3–5).

### Material

SAM-PCZ18739 and SAM-PCZ18741 from an unspecified horizon at Mkwayane (Umkwelane Hill), St Lucia Formation, Santonian or Campanian; SAM-PCZ17357 and

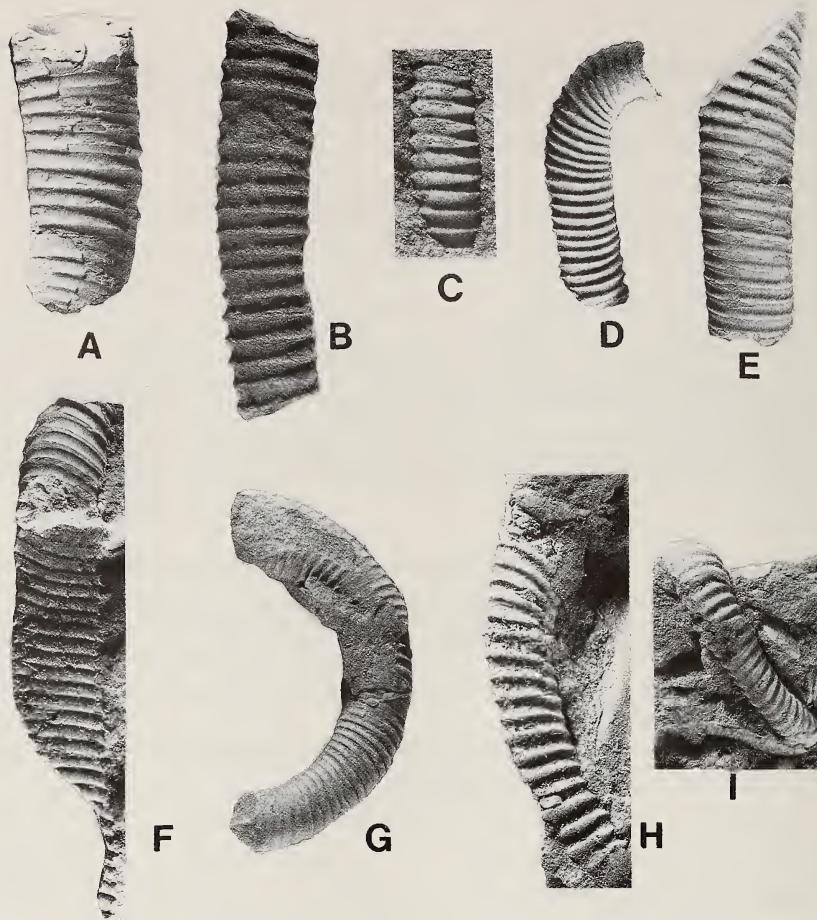


Figure 56

A-B, D-F. *Glyptoxoceras octocostatum* (Collignon, 1969). A. SAM-PCZ18739. D. SAM-PCZ18741. Both from Mkweyane (Umkwelane Hill), KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. B. SAM-PCZ18740 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. E-F. SAM-PCZ17357 from locality 105, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian. C. *Glyptoxoceras rugatum* (Forbes, 1846). SAM-PCZ17358 from below the base of the Uloa Formation at Monzi, KwaZulu, St Lucia Formation, Maastrichtian. G. *Neoglyptoxoceras collignonii* nom. nov. SAM-PCZ18742 from locality 109, KwaZulu, St Lucia Formation, Campanian II or III. H-I. *Scalarites* sp. H. SAM-PCZ18738. I. SAM-PCZ7961, both from locality 72, KwaZulu, St Lucia Formation, Coniacian II. All  $\times 1$ .

SAM-PCZ18740 (ex Z2071) from locality 105, St Lucia Formation, uppermost Santonian or basal Campanian; SAM-PCZ9923 from locality 18, KwaZulu, St Lucia Formation, Santonian.

#### Description and discussion

The material consists of curved fragments of a species which may be referred to *G. octocostatum*. The whorl section is rounded and, as the name implies, ornament consists of

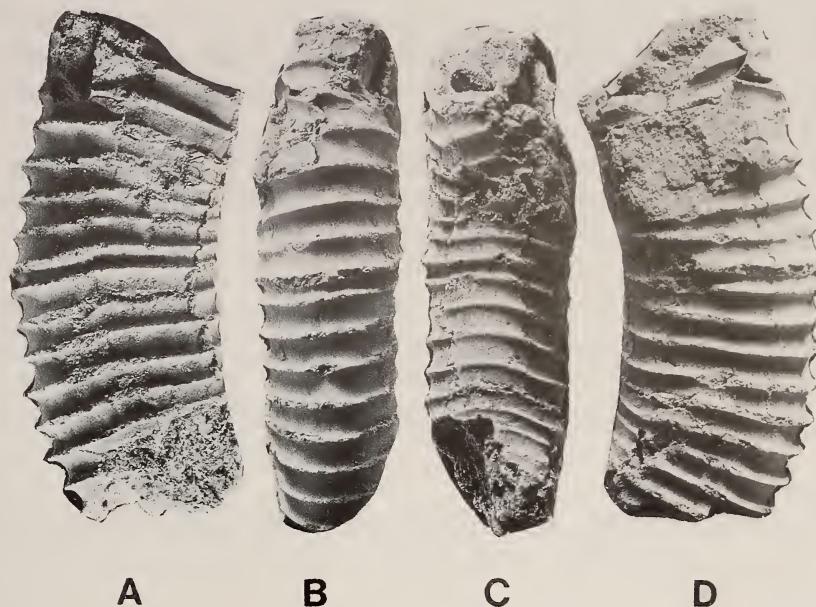


Figure 57

*Glyptoxoceras texanum* Kennedy, Landman & Cobban, 2001. SAM-PCZ12955 (ex H179/20) from locality 6, KwaZulu, St Lucia Formation, upper Santonian or lower Campanian.  $\times 1$ .

about eight sharp ribs per whorl height. As indicated by Kennedy & Henderson (1992) and Henderson *et al.* (1992), *G. indicum* is a typical Maastrichtian species, and not conspecific with the Santonian and/or Campanian material referred to this species by e.g. Klinger (1976: 79).

#### Occurrence

Uppermost Santonian and/or basal Campanian of Pondoland and KwaZulu, and lower Campanian Madagascar.

*Glyptoxoceras texanum* Kennedy, Landman & Cobban, 2001

Fig. 57

1976      *Diplomoceras (Glyptoxoceras) subcompressum* (Forbes); Klinger, p. 80, pl. 34 (fig. 6).  
 2001      *Glyptoxoceras texanum* Kennedy, Landman & Cobban, p. 7, (fig. 4).

#### Material

SAM-PCZ12955 (ex H179/20) from spoil heaps at excavations for a bridge at locality 6, St Lucia Formation, upper Santonian or basal Campanian.

#### Description and discussion

The specimen differs from all others referred to *Glyptoxoceras* in southern Africa in having a distinctly compressed whorl section ( $Wb:Wh = 0.7$ ), about six ribs per whorl

height and a distinct constriction. Even though we only have a single specimen, the dimensions, ornamentation and stratigraphic occurrence are identical to the species recently described by Kennedy *et al.* (2001: 7) from the top of the Blossom Sand in Texas as *Glyptoxoceras texanum*.

Klinger (1976: 80) previously referred the specimen to *G. subcompressum*, but that species has thus far only been accurately recorded from the upper Maastrichtian and therefore can not be the same as the KwaZulu specimen.

#### *Occurrence*

Uppermost Santonian or basal Campanian of KwaZulu, upper Santonian of Texas.

#### Genus *Scalarites* Wright & Matsumoto, 1954

##### *Type species*

*Helicoceras scalare* Yabe (1904: 9, pl. 3 (fig. 2)), by original designation of Wright & Matsumoto (1954: 115).

##### *Diagnosis*

Early straight shaft with constrictions followed by loose elliptical coils ornamented by simple ribs with occasional flared, non-tuberculate ribs and occasional constrictions.

##### *Discussion*

*Scalarites* is amongst the oldest diplomoceratids. *Scalarites densicostatus* Matsumoto (1977: 349, pl. 57 (fig. 1), pl. 61 (fig. 6)) already occurs in the middle Turonian. It differs from other *Scalarites* in having *Diplomoceras*-like coiling. Matsumoto (1977: 350) suggested that it might be ancestral to *Polyptychoceras obstrictum*.

Differences between *Glyptoxoceras* and *Scalarites* may be slight. We suspect that some of the Coniacian and Santonian ‘*Glyptoxoceras*’ may be representatives of *Scalarites*.

##### *Occurrence*

The genus first appears in the middle Turonian and persists to the Santonian. It is best known from Hokkaido, but is also known from California, Morocco, northern Germany, Colombia and KwaZulu.

#### *Scalarites* sp. Fig. 56H–I

##### *Material*

SAM-PCZ18738 (ex SAS-A1997) and SAM-PCZ7961, both from locality 72, St Lucia Formation, Coniacian II.

### Description and discussion

Two body chamber fragments of what appear to be *Scalarites* are available. SAM-PCZ118738 is associated with an evolute peroniceratid. Both specimens are crushed, but the whorl section seems to be higher than wide. Ornament consists of rounded, prorsiradiate ribs, c. three per whorl height. Towards the larger end, the ribs become progressively prorsiradiate.

### Occurrence

Coniacian II of KwaZulu.

Genus *Neoglyptoxoceras* Collignon, 1969  
(= *?Epiglyptoxoceras* Collignon, 1969)

### Type species

*Neoglyptoxoceras magnificum* Collignon (1969: 30, pl. 523 (fig. 2065), p. 35, pl. 526 (figs 2074–2075)) by original designation of Collignon (1969: 35).

### Diagnosis

*Neoglyptoxoceras* forms large, loose open criocone to aspinoceratid coils; some may form a low, loose helix. It is ornamented by ribs only and may have a very complex suture line. The whorl section varies from ovoid to circular. No constrictions have been observed.

### Discussion

The main difference between *Neoglyptoxoceras* and *Glyptoxoceras* is the larger size of the former. A detailed discussion of the genus and its affinities are given by Klinger & Kennedy (This volume 110 (4)).

### Occurrence

Lower and middle Campanian of Madagascar and middle Campanian of KwaZulu.

*Neoglyptoxoceras collignonii* nom. nov.

Fig. 56G

1970      *Neoglyptoxoceras sertum* (Müller & Wollemann); Collignon, p. 15, pl. 613 (figs 2286–2288).  
 1970      *?Neoglyptoxoceras* sp. aff. *sertum* (Müll. et Woll.); Collignon, p. 15, pl. 613 (fig. 2289).  
 2003      *Neoglyptoxoceras* sp. cf. *N. sertum* Collignon 1969 non Müller & Wolleman, 1906;  
               Klinger & Kennedy, fig 10c.

### Type

The holotype is the specimen figured by Collignon (1970, pl. 613 (fig. 2286)) from the middle Campanian of Gisement 203, Coupe d'Andimaka, Belo sur Tsiribihina, Madagascar.

### *Etymology*

Named after the late General M. Collignon.

### *Material*

SAM-PCZ18742 from locality 109C, KwaZulu, St Lucia Formation, Campanian III?

### *Description and discussion*

Half a criocone whorl with a rib density of about 6 per whorl height appears identical with Collignon's figured material from the middle Campanian of Madagascar.

Collignon (1970: 15) originally identified his Madagascan specimens with Müller & Wollemann's (1906: 20, pl. 9 (fig. 3), pl. 10 (figs 1-4)) *Crioceras sertum*, as *Neoglyptoxoceras*. Müller & Wollemann (1906: 21), however, clearly state that in later stages of growth, larger, flared ribs start appearing at regular intervals. Because of this latter feature, *Crioceras sertum* cannot be referred to *Neoglyptoxoceras*. This type of ornamentation is reminiscent of *Eubostrychoceras* (*Amapondella*).

The coiling of *N. collignoni* is very similar to some *Eubostrychoceras*, but the generally much larger size may separate it from loosely coiled *Eubostrychoceras*.

### *Occurrence*

Middle Campanian of Madagascar and Campanian III of KwaZulu.

Genus *Neocrioceras* Spath, 1921b

Subgenus *Neocrioceras* (*Neocrioceras*) Spath, 1921b

### *Type species*

*Neocrioceras* cf. *spinigerum* Jimbo, 1894 by original designation of Spath (1921b: 51).

### *Diagnosis*

Initial loose helix followed by open spiral and some with J-shaped body-chamber. Ribs, some stronger and with lateral and ventral tubercles.

### *Discussion*

Spath erected the genus *Neocrioceras* and designated as 'genotype' (type species) part of a helically coiled fragment which he tentatively identified as *Neocrioceras* cf. *spinigerum* (here refigured as Fig. 63C-E). This specimen is from the type locality of the Mzamba Formation in Pondoland, presumably from the upper Santonian part of the section. It is, in fact, part of *N. (Schlueterella) compressum* Klinger, 1976. Diener (1925: 192) subsequently designated *Neocrioceras* (*N.*) *spinigerum* Jimbo (1894: 184, pl. 24 (figs 1-1b)) as type species of *Neocrioceras*. This has caused considerable confusion in interpreting *Neocrioceras*. Matsumoto (in Matsumoto *et al.* 1986) described and figured a suite of specimens of *Neocrioceras* (*N.*) *spinigerum* from the Santonian of Hokkaido. These show that *N. (N.) spinigerum* is coiled in an open, planispiral criocone throughout. This, however, is in contrast to Spath's original concept of the genus—i.e. helical early

whorls and possibly an uncoiled straight shaft (as in *Ancyloceras pseudoarmatum* Schlüter 1876: 164, pl. 43 (figs 8–9)). Apart from the original material described by Spath, no additional specimens of *Neocrioceras* cf. *spinigerum* (i.e. *N. (Schlueterella) compressum*) have been found at Mzamba.

#### *Occurrence*

*Neocrioceras* s.s. is only definitely known from the Turonian to Santonian and possibly lower Campanian of Japan and Saghalian, and the Coniacian of KwaZulu. Records from the lower Santonian of the Gosau as *Neocrioceras maderi* by Immel *et al.* (1982: 24, pl. 9 (fig. 2), pl. 11 (figs 1–2)) are regarded as doubtful *Neocrioceras* by Matsumoto in Matsumoto *et al.* (1986: 468), a view not supported here.

#### *Neocrioceras (Neocrioceras) annelisae* sp. nov.

Fig. 58

#### *Type*

Holotype by monotypy is SAM-PCZ9809 from locality 72, KwaZulu, St Lucia Formation, Coniacian III.

#### *Etymology*

Named after Annelise Crean (S.A. Museum) who patiently prepared the specimen.

#### *Description*

The holotype is septate throughout. Coiling appears to be in an open criocone. The whorl section is elliptical, higher than wide with a Wb:Wh ratio of 16:21 (0.76) and 20:24 (0.83) at the smaller and larger ends respectively.

The ornamentation of the species is very distinctive. Fine ribs occur on the flanks and over the dorsum. These are slightly prorsiradiate on the flanks and radial over the dorsum and uniformly strong throughout. A row of large clavate tubercles occurs on either side of the venter, and a second row just above mid-flank. The ventral and ventrolateral tubercles are arranged in sets of three. Starting from the abapertural end, the first ventral tubercle is smallest, the second about twice as large as the first and distinctly clavate. The third is the largest of the three and about twice as large as the preceding tubercle and distinctly clavate. It has a groove running along the lateral flank, suggesting a bipartite origin. The ventrolateral tubercles show a similar increase in size, but they are much smaller than the ventral ones. The third ventrolateral tubercle also shows a slight radial groove on the flanks, similar to that of its ventral counterpart.

Ventrally, the tubercles are connected in a series of adaperturally curved looped ribs. The ventral and ventrolateral tubercles are joined by irregularly distributed ribs; some are connected by irregular loops whereas others are connected in a zigzag fashion. About three to four intermediary ribs occur between these sets of tubercles. Dorsally, two to four ribs connect with the ventrolateral tubercles.

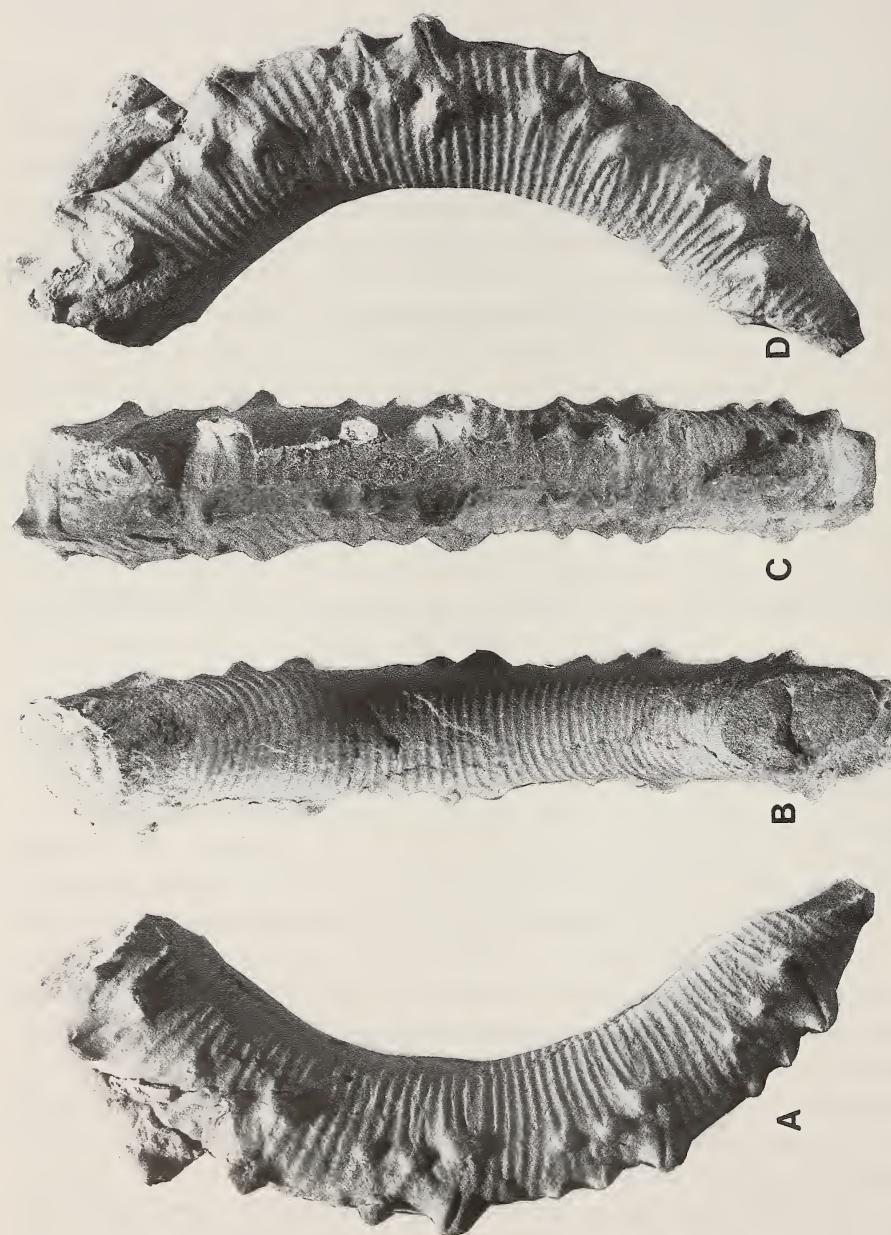


Figure 58

*Neocrioceras (Neocrioceras) annelisae* sp. nov. The holotype, SAM-PCZ9809 from locality 72, KwaZulu, St Lucia Formation, Coniacian III.  $\times 1$ .

### Discussion

Even though this species is represented by a single specimen only, the unique mode of ornamentation consisting of sets of three tubercles arranged in order of increasing size clearly distinguishes *N. (N.) annelisae* from all other representatives of *Neocrioceras*. The open, criocone coiling and lack of clearly thickened ribs suggests that the species is best referred to *Neocrioceras* s.s. rather than to *N. (Schlueterella)*.

The closest match with the present species is *Kawashitaceras dentatum* Matsumoto & Obata (1981: 115, pl. 1 (fig. 1), pl. 2 (fig. 1)); also Matsumoto (1984, fig. 1) from the upper Turonian of Hokkaido. Here, however, the ventral and ventrolateral tubercles are each situated on a wide base and their crests are serrated and staggered.

### Occurrence

Coniacian III of KwaZulu.

Subgenus *Neocrioceras (Schlueterella)* Wiedmann, 1962

#### Type species

*Ancyloceras pseudoarmatum* Schlüter 1872 by original designation of Wiedmann (1962: 205).

#### Diagnosis

Open spiral or helix followed by ancyloceratid coiling. Tuberculate ribs, with four rows of tubercles, more prominent than intercalatory, non-tuberculate ones.

### Discussion

Matsumoto & Miyauchi (1984: 59) and Matsumoto in Matsumoto *et al.* (1986: 469) have discussed the affinities of *Neocrioceras (Schlueterella)* and *Neocrioceras (Neocrioceras)*. Some species, which had been referred to *Neocrioceras (Schlueterella)*, e.g. *N. (S.) riosi* Wiedmann (1962: 205, pl. 12 (fig. 7)) from the Campanian of northern Spain and *S. multinodosum* (Schlüter 1872: 106, pl. 32 (figs 1–2)); Wright 1979: 293, pl. 2 (figs 4–5)) from the Turonian of Germany and England are best referred to *Pseudoxybeloceras*, as pointed out in part by Klinger (1976: 74).

### Occurrence

The subgenus first appears in the middle Coniacian of Wyoming, but is most common in the Santonian to Campanian, with records from KwaZulu, Pondoland, Madagascar, California, northern Germany, Sweden, France, Romania and Hokkaido.

*Neocrioceras (Schlueterella) compressum* Klinger, 1976

Figs 59, 60A–C, 61

1921b *Neocrioceras* cf. *spinigerum*, Jimbo sp.; Spath, p. 52, pl. 7 (fig. 6a–c).

1976 *Neocrioceras (Schlueterella) compressus* Klinger, p. 74, pl. 33 (fig. 5), text-figs 8j, 10g.

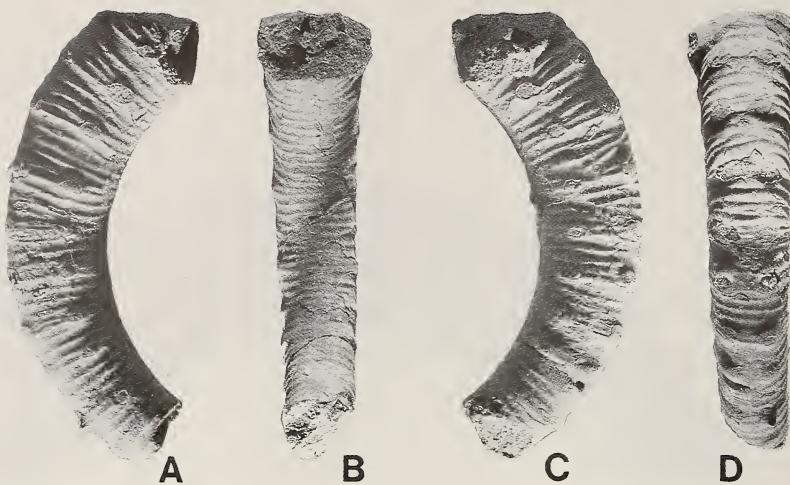


Figure 59

*Neocrioceras (Schlueterella) compressum* Klinger, 1976. SAM-PCZ17363 from locality 74, KwaZulu, St Lucia Formation, Santonian I.  $\times 1$ .

1982 *Neocrioceras (Schlueterella) compressum* Klinger; Immel *et al.* p. 25, pl. 9 (fig. 3), pl. 10 (figs 1–4), pl. 11 (fig. 3).

1991b *Neocrioceras (Schlueterella) compressum* Klinger; Kennedy & Cobban, p. 65, pl. 10 (figs 1–2), pl. 12 (figs 4–7), text-fig. 25c.

1995 *Neocrioceras (Schlueterella) compressum* Klinger; Kennedy, p. 430, pl. 27 (figs 13–15), pl. 29 (figs 4–7).

#### Type

Holotype is SAS-19/1, the specimen figured by Klinger (1976, pl. 33 (fig. 5), text-figs 8j, 10g) from locality 94, KwaZulu, St Lucia Formation, Santonian I.

#### Material

Apart from the holotype, the specimen described and figured by Spath (1921b, pl. 7 (figs 6a–c)) as *Neocrioceras* cf. *spinigerum* and SAM-PCZ17363 from locality 74, Santonian I and SAM-PCZ17364 from locality 79, Coniacian V, KwaZulu, St Lucia Formation.

#### Description and discussion

It is now clear that Spath unknowingly had *Schlueterella* in mind when he proposed the genus *Neocrioceras*. The 'genotype' (type species) of Spath's *Neocrioceras* is in fact a good example of *Neocrioceras (Schlueterella) compressum* Klinger, 1976. A crushed body chamber fragment from locality 79 (Fig. 60A–C) has ornament comparable to that described and figured by Immel *et al.* (1982) from the Santonian of Austria, especially their (1982, pl. 10 (fig. 3)) specimen with few intercalatory ribs.

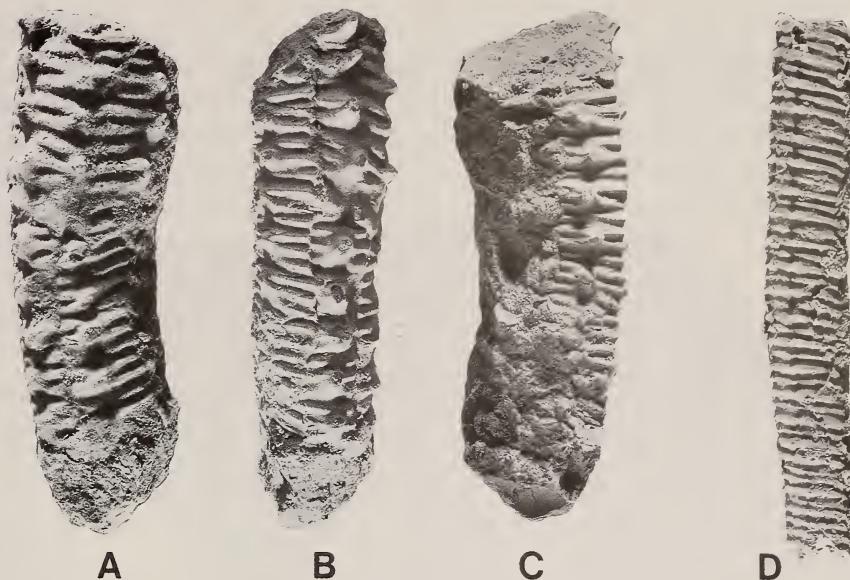


Figure 60

A–C. *Neocrioceras (Schlueterella) compressum* Klinger, 1976. SAM-PCZ17364 from locality 79, KwaZulu, St Lucia Formation, Coniacian V. D. *Pseudoxybeloceras (Pseudoxybeloceras) quadrinodosum* (Jimbo, 1894). SAM-P1411 from an unspecified horizon at the type section of the Mzamba Formation, the Mzamba River Estuary, Eastern Cape Province, locality 1, upper Santonian or lower Campanian. Both  $\times 1$ .

#### Occurrence

Upper Coniacian and lower Santonian of KwaZulu, lower Santonian of Austria, middle Coniacian of Wyoming and Santonian of California. It is also known, but as yet undescribed from Japan (Matsumoto & Miyauchi 1984: 63) and Madagascar (H.C.K. pers. ob.) (Fig. 61).

Subfamily Polyptychoceratinae Matsumoto, 1938

(*nom. transl.* Wiedmann, 1962, *ex* Polyptychoceratidae Matsumoto, 1938)

Genus *Pseudoxybeloceras* Wright & Matsumoto, 1954

#### Type species

*Hamites quadrinodosus* Jimbo, 1894 by original designation of Wright & Matsumoto (1954: 119).

#### Diagnosis

Shell consists primarily of straight or curved shafts connected by U-bends. Ribbing may be bi- or quadrituberculate; in some forms major ribs develop on the body chamber.



Figure 61

*Neocrioceras (Schlueterella) compressum* Klinger, 1976, GD, unregistered, a giant specimen from Gisement 275, middle Santonian of Madagascar.  $\times 1$ .

### Discussion

We follow Klinger (1976) in regarding *Parasolenoceras* Collignon, 1969 and *Christophoceras* Collignon, 1969 (of which *Cyphoceras* Ward & Mallory 1977 is a synonym) as subgenera of *Pseudoxybeloceras*. This arrangement was also followed by Matsumoto & Morozumi (1980: 19). The genus *Lewyites* Matsumoto & Miyauchi, 1984 (type species *Idiohamites* (?) *orionensis* Lewy, 1969) may possibly also be included as a subgenus in *Pseudoxybeloceras*.

### Subgenus *Pseudoxybeloceras* (*Pseudoxybeloceras*) Wright & Matsumoto, 1954

#### Type species

*Hamites quadrinodosus* Jimbo, 1894 by original designation of Wright & Matsumoto (1954: 119).

#### Diagnosis

Straight or curved shafts connected by U-bends. Ribbing uniform throughout. Initial ornament may consist of ventral tubercles on ribs only, but soon changes to ventral and ventrolateral on every rib.

#### Occurrence

The subgenus has been recorded from the upper Turonian to possibly Maastrichtian with records from Austria, Germany, France, Romania, Pondoland, KwaZulu, Madagascar, New Zealand, U.S. Western Interior, California, British Columbia, Alaska, Hokkaido and Saghalien.

### *Pseudoxybeloceras* (*Pseudoxybeloceras*) *quadrinodosum* (Jimbo, 1894)

Figs 60D, 62

1894     *Hamites quadrinodosus* Jimbo, p. 39, pl. 7 (figs 3–4).  
 1921     *Hamites amapondensis* Van Hoepen, p. 15, pl. 3 (figs 5–6), text-fig. 9.  
 1921b    *Oxybeloceras*? cf. *quadrinodosum* (Jimbo); Spath, p. 50, pl. 7 (figs 2a–b).  
 1954     *Pseudoxybeloceras quadrinodosum* (Jimbo); Wright & Matsumoto, p. 120, pl. 7 (fig. 6), text-figs 6, 9–12.  
 1974     *Pseudoxybeloceras quadrinodosum* (Jimbo); Szász, p. 193, pl. 1 (figs 1–4), pl. 2 (figs 1–3), pl. 3 (fig. 1), text-fig. 2.  
 1976     *Pseudoxybeloceras* sp. A. Klinger, p. 77, pl. 34 (fig. 1a–b).  
 1977     *Pseudoxybeloceras quadrinodosum* (Jimbo); Matsumoto, p. 345, pl. 57 (fig. 2), pl. 61 (fig. 4).  
 1977     *Pseudoxybeloceras quadrinodosum* (Jimbo); Ward & Mallory, p. 611, text-fig. 2.  
 1982     *Pseudoxybeloceras quadrinodosum* (Jimbo); Szász, p. 49, pl. 2 (figs 2a–b), pl. 3 (fig. 3a–b).  
 1994     *Pseudoxybeloceras amapondense* van Hoepen; Cooper, (figs 1h–i, 2).

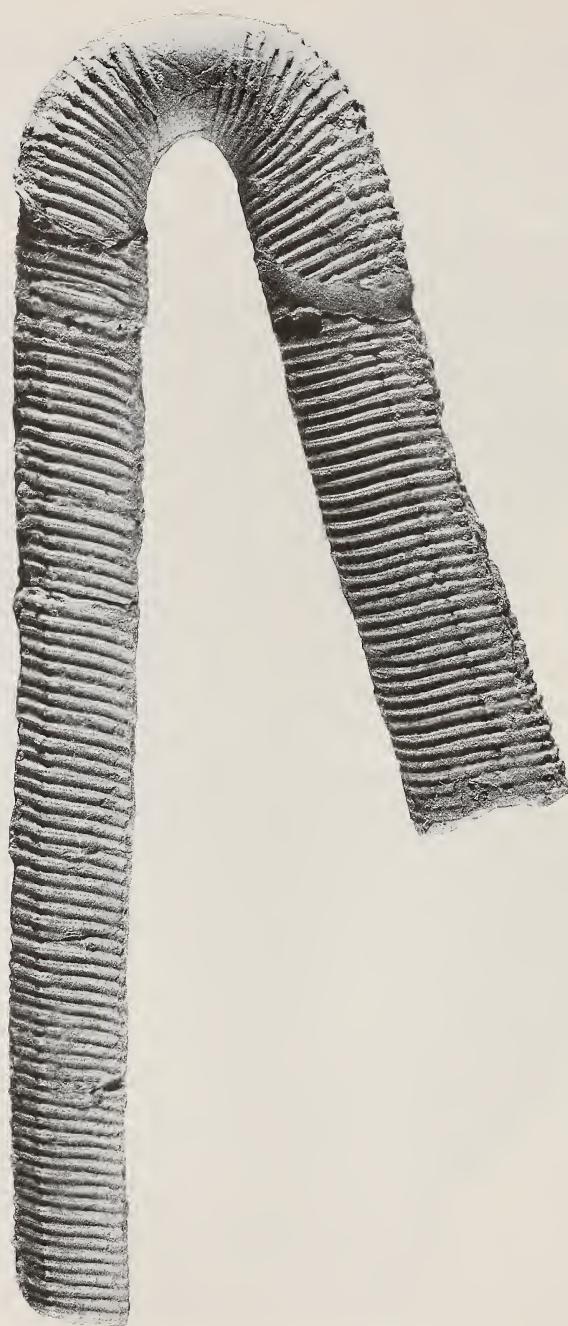


Figure 62

*Pseudoxybeloceras (Pseudoxybeloceras) quadrinodosum* (Jimbo, 1894). SAM-PCP18744 (ex Cape of Good Hope Geological Commission collection). From an unspecified horizon at the type section of the Mzamba Formation at the Mzamba River Estuary, Eastern Cape Province, locality 1, upper Santonian or lower Campanian.  $\times 0.7$ .

### Type

Lectotype by subsequent designation of Wright & Matsumoto (1954: 120) is the specimen figured by Jimbo (1894, pl. 7 (fig. 3)), housed in the collections of the University Museum, University of Tokyo, nr MM7524-1 from the Santonian?–Campanian of the Chiptanshibets on the Tumbets River, Kitami Province, Hokkaido.

### Material

SAM-PCP18744 and SAM-P1411, both from an unspecified horizon at locality 1, the type section of the Mzamba Formation at the Mzamba River Estuary, Pondoland, Eastern Cape Province, Mzamba Formation, probably Santonian III.

### Description

The larger of the two specimens, SAM-PCP18744 (Fig. 62), consists of two straight shafts, connected by an open U-bend, such that they are not strictly parallel, but slightly divergent. This appears to be the specimen from the Geological Survey, Cape Town, mentioned by Spath (1921b: 51) and refigured by Cooper (1994, fig. 2).

The whorl section is oval, higher than wide, with a rounded dorsum and flanks, but flattened in the intertubercular area over the venter and the ventrolateral third. Maximum width is at mid-flank. Ornament consists of fine, single ribs, each bearing four rows of small, pointed tubercles; one pair on the venter and the other at the ventrolateral third of the flanks. Ribbing on both shafts is prorsiradiate, but the degree of inclination and density varies slightly. At the smaller end there are 9 distinctly prorsiradiate ribs per whorl height; at the biggest end there are nearly 12 rectiradiate ribs per whorl height. Towards, and in the bend, ribbing changes from rectiradiate to rursiradiate.

The smaller specimen, SAM-P1411 (Fig. 60D), is slightly curved, and shows irregular development of the ventrolateral row of tubercles. These only occur on alternate ribs and are irregularly displaced on either side.

### Discussion

The smaller specimen (Fig. 60D) was originally identified as *Pseudoxybeloceras?* sp. A by Klinger (1976: 77) because of the irregular tuberculation. However, seen in association with the adult specimen, it seems that this feature is merely part of the juvenile ornamentation. In the most comprehensive discussion of *P. (P.) quadrinodosum* so far, Matsumoto (1977: 345–347) also describes the early ornament. Here, however, the bituberculate stage passes directly to the quadrituberculate stage without intermediary bituberculate ribs as in the Pondoland specimen. The early stages of *P. (P.) quadrinodosum* thus show a combination of *Parasolenoceras* (type species *Parasolenoceras splendens* Collignon 1969: 44, pl. 530 (fig. 2087)) and *Christophoceras* (type species *Christophoceras ramboulai* Collignon 1969: 47, pl. 531 (fig. 2093)) features and further support our view that these could be included as subgenera of *Pseudoxybeloceras*; as also suggested by Matsumoto & Morozumi (1980: 19) and tentatively by Ward & Mallory (1977: 611) (as *Cyphoceras* Ward & Mallory, 1977) and most recently by Wright (1997: 253).

*Hamites amapondensis* Van Hoepen (1921: 15, pl. 3 (figs 5–6), text-fig. 9) is a clear

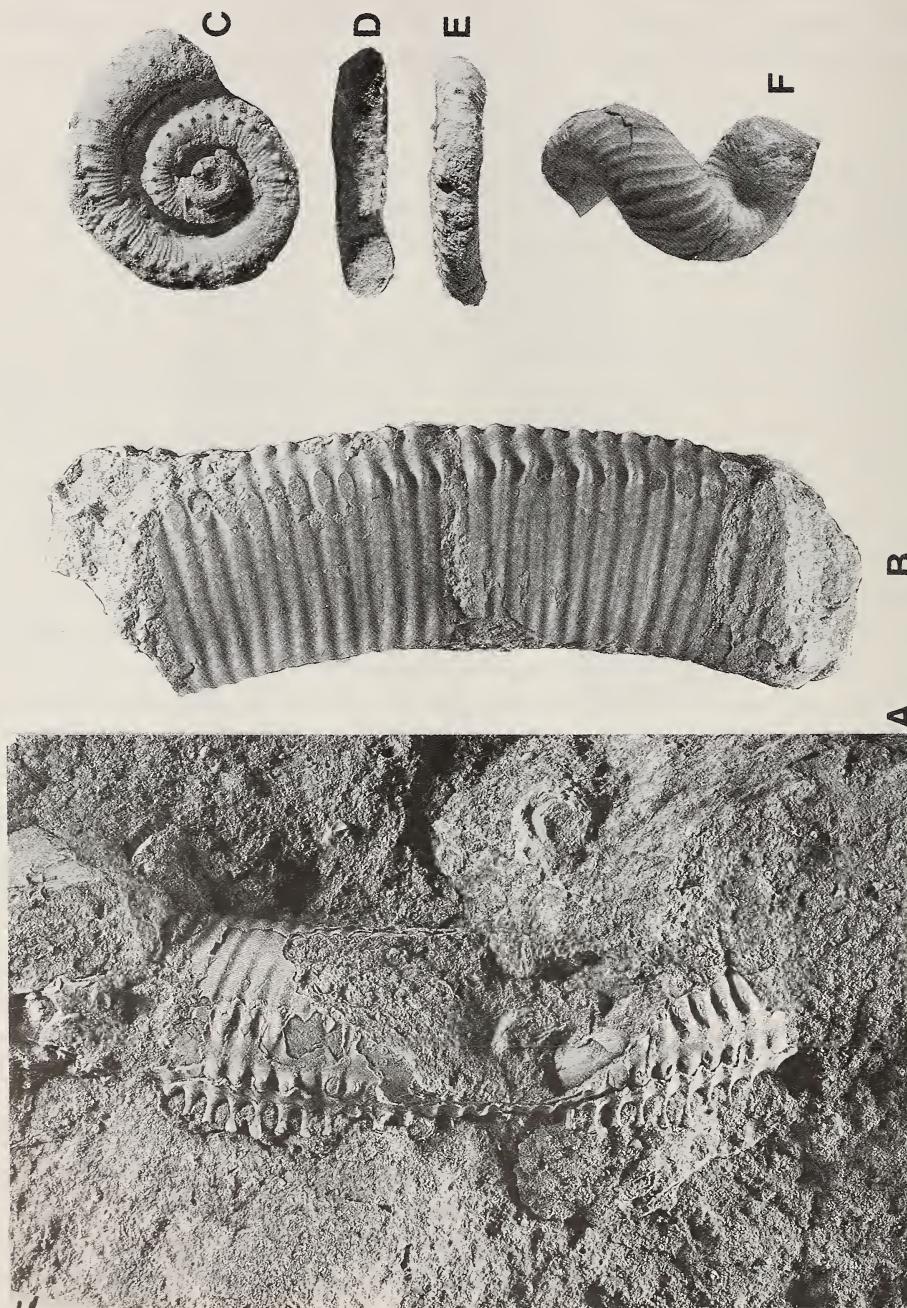


Figure 63

synonym of *P. (P.) quadrinodosum*, as Van Hoepen (1921: 16) had tentatively suggested. Differences quoted by him, e.g. details of the suture line, rib density and whorl section are all within the limits of intraspecific and ontogenetic variation.

*Oxybeloceras?* cf. *quadrinodosum* in Spath (1921b: 50, pl. 7 (fig. 2a–b)) with ventral tubercles only, is merely a juvenile of *P. quadrinodosum* as shown by the descriptions of Matsumoto (1977).

#### Occurrence

So far none of the Pondoland specimens have been accurately localized, but they probably occur in the upper Santonian. In Romania, Szasz (1974, 1982) records the species from the upper Campanian. The Japanese specimens are probably of Santonian age, but could be Campanian (Matsumoto 1977: 346). This seems to indicate a Santonian to Campanian age for the species in Japan, Romania and Pondoland.

*Pseudoxybeloceras (Pseudoxybeloceras) matsumotoi* Collignon, 1965

Fig. 63A–B

1965 *Pseudoxybeloceras matsumotoi* Collignon, p. 12, pl. 419 (fig. 1731).  
 1965 *Diplomoceras (Glyptoxoceras) subcompressum* Forbes; Collignon, p. 13, pl. 419 (fig. 1732).  
 1976 *Pseudoxybeloceras (Pseudoxybeloceras) matsumotoi* Collignon; Klinger, p. 76, pl. 33 (fig. 6).  
 2003 *Pseudoxybeloceras matsumotoi* Collignon; Klinger & Kennedy (This volume 110 (5)), p. 199, figs 1–10.

#### Type

Lectotype designated by Klinger & Kennedy (2003: 214) is the specimen figured in Collignon (1965, pl. 419 (fig. 1731)) GD11731 from the lower or middle Coniacian of Beantaly (Belo sur Tsiribihina), Madagascar.

#### Material

SAM-PCZ18747 (ex SAS-92/1) from bed 1 at locality 92, KwaZulu, St Lucia

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Fig. 63 (see facing page). A–B. *Pseudoxybeloceras (Pseudoxybeloceras) matsumotoi* Collignon, 1965.

A. SAM-PCZ18747 (ex 92/1) from locality 92, KwaZulu, St Lucia Formation, Coniacian II. Note the distinct spatulate endings of the spines. B. NMB-PCZ18743 from locality 145, KwaZulu, St Lucia Formation, Coniacian II. C–E. *Neocrioceras (Schlueterella) compressum* Klinger, 1976. Natal Museum, Durban collections, the original of Spath's (1921b: 52, pl. 7 (Figs 6a–c)) *Neocrioceras* cf. *spinigerum*, and the 'genotype' of *Neocrioceras* sensu Spath (1921b: 51) from an unspecified horizon at the type locality of the Mzamba Formation, Mzamba River Estuary, Eastern Cape Province, locality 1, upper Santonian or lower Campanian. F. *Eubostrychoceras (Eubostrychoceras) zulu* sp. nov. SAM-PCZ18709, a paratype from locality 72, St Lucia Formation, Coniacian II. A–E × 1; F × 2.

Formation, Coniacian II; NMB-PCZ18743 from locality 145, KwaZulu, St Lucia Formation, Coniacian II.

#### Description

The specimen originally figured by Klinger (1976, pl. 33 (fig. 6)) is here refigured (Fig. 63A) to show the spatulate shape of the hollow spines, where preserved. The other specimen, NMB-PCZ18743 (Fig. 63B) is virtually identical to the lectotype. The whorl section is elliptical ( $Wb:Wh = 21.5:30.4$  (0.71)). Ornament consists of predominantly single, radial ribs, numbering about 8 or 9 per whorl height. Each bears a small pair of ventrolateral, radially elongated tubercles and a larger pair of ventral tubercles. As mentioned above, in shelly preservation these bear long, spatulate, hollow spines.

#### Discussion

Hollow spines are rarely preserved in heteromorphs. These may be quite variable, but are generally pointed and sealed off from the rest of the shell by a convex septum. Spatulate spines that are somewhat similar to those of *P. (P.) matsumotoi* have been observed in *Hyphantoceras (H.) reussianum* (see e.g. Metzendorf 1992, pl. 1 (figs 7–8)) and *P. (P.) aff. lineatum* (In: Olivero 1988, fig. 3C–D).

A full discussion of the ontogeny, shell structure and differential preservation of internal moulds of the phragmocone and body chamber respectively in *P. matsumotoi* is given by Klinger & Kennedy (This volume 110 (5)).

#### Occurrence

Rare in Coniacian II of KwaZulu, common in the lower and middle Coniacian of Madagascar.

### Genus *Spiroxybeloceras* Kennedy & Cobban, 1999

#### Type species

*Ptychoceras meekanum* Whitfield, 1877: 44, illustrated by Whitfield 1880, pl. 16 (figs 1–2) from the Pierre Shale, Wyoming, by original designation of Kennedy & Cobban (1999: 74).

#### Diagnosis

Early stage loose, planispiral, followed by two parallel shafts barely in contact. Ornament consists of narrow, sharp ribs that bear small pointed tubercles on the venter.

#### Discussion

There is some confusion about the validity of three genera with very similar adult stages: *Solenoceras* Conrad, 1860 (type species *Hamites annulifer* Morton, 1841: 109), *Oxybeloceras* Hyatt, 1900 (type species *Ptychoceras crassum* Whitfield, 1880: 459) and *Spiroxybeloceras* Kennedy & Cobban, 1999 (type species *Ptychoceras meekanum* Whitfield, 1877). According to Kennedy & Cobban (1993a: 142), *Solenoceras* and

*Oxybeloceras* differ in that: (1) '*Solenoceras* consists of two straight parallel shafts, lacking the initial planispiral of *Oxybeloceras*'; (2) *Solenoceras* has 'the shafts closely adpressed for all their length'; (3) 'constrictions with associated flared ribs occur on the body chamber and phragmocone'; (4) 'The ribs bearing tubercles are weaker than in *Oxybeloceras* and the tubercles may efface'.

*Spiroxybeloceras* is similar to *Solenoceras*, but differs in having an early ontogenetic stage consisting of a loose planispiral growth stage, followed by two parallel shafts barely in contact. *Solenoceras*, in contrast, has an early ontogenetic stage consisting of an ammonitella, followed by a straight shaft which is impressed in a second, parallel shaft.

#### Occurrence

*Solenoceras* s.l. occurs in the upper Campanian and lower Maastrichtian, and has been recorded from the Gulf Coast regions of the USA, Angola, Nigeria, Egypt, the Middle East, Spain, Madagascar, KwaZulu and Japan.

#### *Spiroxybeloceras minimus* (Basse, 1931)

Fig. 64

1931      *Hamites (Ptychoceras) minimus* Basse, p. 17, pl. 1 (figs 20–22).  
 ?1931      *Hamites (Ptychoceras) cf. Humei* Douvillé; Basse, p. 18, pl. 6 (figs 9–10).  
 1976      *Solenoceras* sp. cf. *texanum* (Shumard); Klinger, p. 77, pl. 34 (fig. 7).

#### Type

Lectotype here designated is the specimen figured by Basse (1931, pl. 1 (figs 20–22)) from Andrafiavelo, Madagascar.

#### Material

SAM-PCZ17365 (ex SAS-A2083), probably from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. SAM-PCZ7899, SAM-PCZ7900a, b, SAM-PCZ18745–6, SAM-PCZ9890, all from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b.

#### Description

The new material shows the early criocone whorls of the species. Unfortunately these are only preserved as imprints or incomplete secondary infillings. The rest of the shell consists of two slightly curved shafts. The smaller is distinctly impressed into the dorsum of the larger. Ornament consists of fine, sharp-crested ribs. In the curved section connecting the two shafts, the ribs are interrupted over the venter and end in a pair of small ventrolateral tubercles. On the rest of the shell, the ribs are continuous over the venter. Minute tubercles can be seen under oblique lighting on the body chamber shaft.

The species is very small—the total length of the final shaft is 30 mm or less. The mode of occurrence of the material is of interest. One of the specimens, SAM-PCZ7899 is situated in part of the body chamber of *Nostoceras (Bostrychoceras) sanctaeluciense*. In the nodule SAM-PCZ18745–6, at least seven specimens are visible.

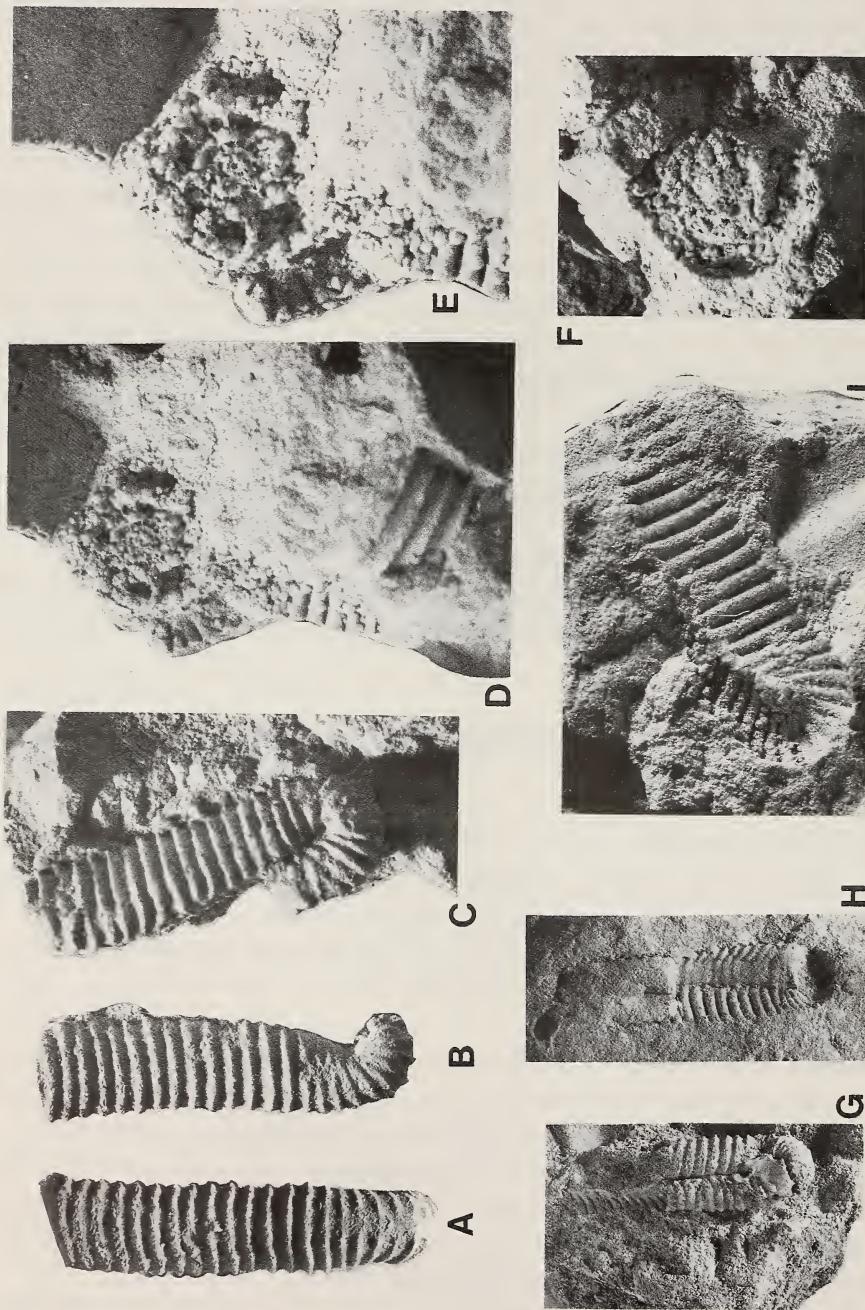


Figure 64

*Spiroxybeloceras minimus* (Basse, 1931). A-B. SAM-PCZ7900a. C. SAM-PCZ7900a. D-F. SAM-PCZ7900b. I. SAM-PCZ18746. All from locality 119, KwaZulu, St Lucia Formation, Maastrichtian a or b. Note the open, criocone early whorls in D-F. A-C, I  $\times 2$ ; G-H  $\times 1$ ; D-F  $\times 4$ . A2083.

### Discussion

The presence of early criocone whorls, first suggested by Whitfield (1892: 273) and substantiated by Lewy (1967: 170, pl. 3 (figs 1–2)) in *Spiroxybeloceras humei humei* (Douvillé, 1929) is further confirmed by the present material.

Klinger (1976: 77) initially identified a single specimen of this genus as *Solenoceras* sp. cf. *texanum* and distinguished it from *S. minimus* (Basse, 1931) on account of the denser ribbing of the latter. Basse's figures (1931, pl. 1 (fig. 20–22)) show very fine tubercles on the final shaft, similar to those in SAM-PCZ7900a. The small size, the impression of the first shaft into the dorsum of the second, and the very fine ventral tuberculation on the final shaft are characteristic of the species.

It is difficult to separate all known species of *Spiroxybeloceras* satisfactorily. Perhaps because of their small size, individuals are not very common in collections. In addition, complete specimens are rare. *S. texanum* (Shumard) (1861: 190) (see Stephenson 1941: 399, pl. 77 (figs 4–5), pl. 79 (figs 1–4)) with which our KwaZulu material had previously been tentatively identified, has very distinct ventral tubercles and is easily separated.

### Occurrence

Lower Maastrichtian, Madagascar and KwaZulu.

## ACKNOWLEDGEMENTS

Financial assistance to Klinger from the Foundation for Research and Development, South Africa, the Service de cooperation et d'action culturelle, France for travelling and subsistence costs in Dijon in 1999, and the Oppenheimer Fund (Oxford University, U.K.) during his stay in Oxford in 2000, and to Kennedy from the trustees of the Sir Henry Strakosh Bequest, Royal Society and Natural Environment Research Council (U.K.) is gratefully acknowledged. Dr J.-H. Delance (Dijon) kindly allowed access to the General M. Collignon collection and loan of material. Some of the Madagascan material illustrated here was donated to H. Klinger by General M. Collignon during his visit to Moirans in 1974. We thank Samantha Black, Ingrid Klinger and Kerwin van Willingh (South African Museum) and the Department of Earth Sciences (Oxford) for technical assistance.

We are grateful to the numerous colleagues who have supplied us with literature, material, photographs and advice. We specially thank Drs W. A. Cobban and N. Landman, and Neal and Peter Larson.

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